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THE BLACK WIDOW SPIDER

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INTRODUCTION

THIS study was undertaken somewhat in the nature of a summer diversion. Our interest in the black widow spider was first aroused by the work of Blair (1) which received considerable publicity during the winter and spring of 1934. When it was found that these spiders were fairly numerous in and around Denver, and a search of the literature indicated that many points concerning their life history and the properties of their venom were not definitely established, a modest research program devoted to their study seemed to promise considerable enjoyment, even though the results might not have an exceedingly great scientific value. Since we could hardly hope to make a specialized study in any one particular field, we decided to explore all of them a little. In consequence, this paper gives findings covering various aspects of the problem. In the first part the appearance of the spider is described, and observations concerning its natural history recorded. In the second, studies concerning the toxicity of the venom, its chemistry, immunology, toxicology, and pathology are reported. Most of the experiments herein reported were carried out during the summer of 1934. However, delay in publication permits inclusion of certain observations and experiments conducted during 1935, especially relating to the production of sheep anti-serum. This work was carried out in cooperation with the E. R. Squibb & Sons Company. The total number of spiders collected has been about 6,500, and some 500 rats have been used.

The literature up to 1932 has been adequately reviewed by Bogen (2); reference to other important work will be made in the appropriate place.

NATURAL HISTORY

Spiders have a life that is vivid and intense, though so unobtrusive that we usually do not see them, or at most pay little attention to them. Specialists find them fascinating as a group because of their anatomical peculiarities, their production of silk, and their habits of preparing snares for prey. Laymen are but little interested in spiders because their apparent economic value is negligible.

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The average person is likely to have an active dislike, if any feeling at all, for spiders. This dislike is not based on justifiable fear. The effect of the bite of a spider has long been a question. The Tarantula, a small wolf spider of southern Europe, figured in early legends because of the music and extravagant bacchic display designed to incite the patient to the violent dancing which was thought to be the sole cure for its bite.

The only other type of spider that has gained a wide and infamous reputation is *Latrodectus*, a genus of the family Theridiidae. Stories of the deadly nature of the bites of these spiders are current among the peoples of all the regions of the world in which they occur. It is difficult to believe that there is no basis in fact for the similar beliefs that have grown up in such widely separated regions as Europe, America, Madagascar, New Zealand, Algeria, and the West Indies. Arachnologists of the old school were inclined to believe that the stories were based on mistaken evidence. Even today some maintain that the reports of the venomous qualities are greatly exaggerated. In the case of *Latrodectus*, incomplete observation gives conflicting evidence. There are authentic reports of bites of this genus of spider being followed by no harmful results. There are equally authentic reports of fatalities, or of more or less serious and disagreeable symptoms, followed by recovery.

The divergence of opinion in regard to the effect of the bite has a simple and reasonable explanation. All spiders have poison glands, which open near the tips of the fangs of the chelicerae. The contents of the poison sac are expelled by muscular action, undoubtedly voluntary on the part of the spider. A "bite", therefore, does not necessarily imply the injection of the venom, but might be entirely harmless. The injection of varying amounts of venom would explain the gradations in the seriousness of the consequences. Nothing but carefully controlled laboratory experiments can give conclusive evidence in a question of this sort.

The fact that the spider has many common names indicates an enforced recognition. The natives of Madagascar know their two species as "Vancoho" and "Mena-vedi". The New Zealand species is the "Katipo". *Latrodectus 13-gattatus* of southern Europe is known as the "Malmignatte". The common American species, *Latrodectus mactans*, was the "Pokomoo" of the Indians, who knew the potency of its venom for making poisoned arrows. Other common names for this spider are the "Black Widow", the "Hourglass", or "Shoebutton" spider.

The Standard Dictionary says that the derivation of *Latrodectus* is apparently from two Greek words meaning "pay received". Jaeger (Dictionary of Latin Combining Forms Used in Zoological Names) derives it from *latro*, Greek, a robber; and *dect(o)*, Greek, to bite, biting, a biter; hence, *Latrodectus*, a robber-biter. *Mactans* is a Latin word meaning "murderous".

Distribution

The most recent review of the distribution of the black widow which has come to our attention is that of Burt (3). This study, combined with that of Bogen, leaves only the following states from which the black widow has not been reported: Oregon, Minnesota, Iowa, Missouri, Wisconsin, Illinois and Vermont. It is almost certainly present in Oregon, in fact, very probably it will be found in every state of the Union. According to Phillips (4), Canadian records are available for the provinces of Alberta, British Columbia, Manitoba and Ontario, and

southward its range in the mainland extends at least to Peru. The species has also been reported from the West Indies.

Habitat

The web of the black widow is an irregular structure, made of coarse, elastic, tough silk. There is usually a central nest or pocket about the size of one's finger to which the spider retreats when she is frightened, and to which she carries many of her meals. The web is evidently being constantly renewed and repaired, as the silk in an abandoned web is dull in appearance, brittle and weak and easily distinguished from the silk in an occupied web. The structure may be of no greater extent than the mouth of a gopher hole, or as much as a yard each way on the surface of a bank, probably being enlarged with the constant renovation. Once the widow has established her web, she is not likely to be found outside of it unless by accident or intent some superior force drives her out. When this happens she shows her discomfort and fear by timid and awkward actions. With the onset of cold weather, however, many reports have reached us of spiders crawling about on walls and floors of dwellings. Apparently the cold has driven them inside and they are hunting a more favorable winter residence.

The location of the web seems to be largely a matter of chance, though in our locality some favorite sites are permanent holes or fissures in a bank, such as the excavations made by swallows in a clay bank; in brick, rock, or trash piles; in sheds, garages, outbuildings and basements; under loose rocks and in eroded holes in granite; in tile roofs, etc. Webs and spiders have been found in abandoned birds' nests in the pine trees of the foothills. Recently we found the whole south side of a new country house in the suburbs of Denver harboring young widows of this season in every possible retreat behind shutters, rain spouts, etc. Webs have been observed in the prickly pear cactus, where they spread about in the branches of the plant, with the central nests in the trash on the ground. In the summer of 1934, perhaps owing to the dryness, these spiders seem to have invaded the residential districts in unusually large numbers, and one of us actually found a mature black widow ensconced behind some books in the library. Reports have come to us of their being found commonly in box cars and a communication from fruit growers on the western slope of the Colorado Rockies stated that grapes were going to waste because pickers refused to work among the spider-infested vines. We have seen the black widow or had reports of her in all parts of Colorado. One was collected at an altitude of 8000 feet near Buffalo Park, the record altitude so far as our personal experience goes, and we collected specimens both in 1934 and 1935 at an altitude of about 7300 feet in Estes Park. Recently we have received from a trustworthy source a record of one taken near the village of Estes Park at an altitude of 8200 feet.

It is evident from the above statements that the spider recognizes few geographic barriers except extreme cold and is also easily satisfied with her local surroundings. At the same time, we have found certain particular locations very densely populated and it would appear that these are the most favorable in insuring survival. As stated, we have collected approximately 6500 spiders. By far the greatest number of these were captured in the foothills country between Denver and Colorado Springs. The hill sides are of disintegrating limestone, forming fissures and clefts in the cliff faces, and with many boulders on the gentler slopes. On the

south slopes of these hills and canyons, nearly every cleft and hole in the cliff has a web across its mouth, nearly every boulder a web along its lower margin. The insect life is not particularly abundant, but in such regions as this one can collect several hundred spiders within a few hours. It should be noted, however, that the size of the spider seems to be in direct proportion to the size of the rock and to collect large specimens one must have the fortitude to turn over large rocks.

The web serves as a snare for the prey on which the spider feeds—flies, beetles, grasshoppers, and the other insects that blunder into it. We have even observed a small mouse entangled and several times have seen the large Western cicada, which is nearly as big as a mouse, a victim. Usually whatever touches the web is securely caught almost at the first contact, and its struggles only tie it the more tightly. Large grasshoppers, however, can kick themselves free and require prompt and energetic measures on the part of the spider. She belongs to the family of "comb-footed" spiders which are distinguished by the presence on the tarsus of the fourth pair of legs of a distinct comb, consisting of a row of strong, curved, and toothed setae. The comb is used for flinging silk, in an almost liquid state, over the entangled prey. It is interesting to see the technique employed in subduing one of the larger grasshoppers, an animal considerably bigger and many times stronger than the spider. What she does is to hog-tie the powerful jumping legs of the victim and after submission is gained in this way she takes her time about administering the fatal bite.

Hibernation

In the vicinity of Denver we have been able to collect specimens in every month of the year. The degree of activity shown by spiders collected in the winter months appears to depend on the temperature; if it is warm, individuals captured behave about as they do in summer; if it is cold, they are more or less torpid. They have been found in winter in all the common places and we have never observed the slightest evidence of special preparation against the cold—nothing in the way of additional web or better protection for the nest. Many of those found under rocks and in trash heaps appear to have made no webs of any kind. In December last year, after a heavy snow with cold nights, we picked up a specimen from the bottom of a pile of tumble-weeds, about as wet and cold a spot as one could imagine. Later, in an unheated room, where half a dozen recently collected spiders were exposed to a temperature of 10 degrees below zero in a sudden cold snap, all were frozen.

Methods of Collecting

Latrodectus is ready both by day and by night for any passing victim and at night is easily spotted with a flashlight. An easy method of collecting from holes in banks and similar places is to tie a beetle to a string eighteen inches or so long with the other end of the string attached to a stick of handy size. When the beetle is dropped into a web, if the spider is hungry, she will at once rush out to capture the struggling insect. Web and spider may then be struck down and the spider transferred by means of forceps to the collecting bottle. Sometimes one may pull out web and egg-sacs so that they dangle just outside the hole. After some time the female may frequently be caught outside in the act of rescuing her eggs and repairing the damage to the web. During the capture of the widow she almost always exhibits the cataleptic

reflex, "playing possum," a protective habit that is common to almost all kinds of spiders, and when picked up by a leg with the forceps she is likely to cast the leg, another protective device that is familiar to spider observers everywhere.

Temperament

The widow is generally found alone, since her fierce and predaceous habits cause her to kill any insect invader, or be killed. The "killer instinct" is apparent in the following description of a typical conflict observed in a web located in a well-lighted hole, about eye level, in a brick-yard bank. The occupant was a large female with two egg-sacs in the upper part of the web. She was hanging back down on one of the sacs—a characteristic position. A small mirror was used to shine light into the hole so that everything might be clearly seen. The observer placed another widow, previously collected, into the outer part of the web. There was no movement for a moment; then the alien oriented herself and moved a short distance into the web. The occupant countered by leaving the egg-sac and advancing a spider's length toward the interloper. Both advanced and stopped alternately until they approached each other in the center of the web. All their movements were deliberate and cautious. There was a moment of absolute stillness, then with a motion too quick for the eye, the occupant threw a shower of thick, sticky silk, which spurted from the spinnerets at the tip of the abdomen and was flung over the invader by a skillful manipulation of the hind legs. The victim was rapidly rolled over and over in a net until it was completely covered like a mummy. It was only then, when the risk was past and all secure, that the poison bite was administered.

Contests staged in the laboratory established the fact that a bite upon another spider causes paralysis immediately, but does not necessarily produce death. Victims removed from the web after they were helpless and all prepared for the victor to begin feeding, were found to recover their powers of motion after several hours, and to be apparently normal the next day. In contrast to the fierce nature of the spider toward others of her kind, is the extreme timidity which she exhibits toward unnatural disturbances of her web, such as might be caused by a collector. At the first molestation of the web, she retreats with incredible speed into the central nest, and does not venture out again for hours. We have never seen the slightest attempt at defense, to say nothing of aggression, on her part under such circumstances.

Reproduction

In mid-summer nearly every web of *Latrodectus* that is found is occupied by a mature female guarding her eggs, and one hardly ever sees a male. As fall approaches the mature females decline in number and the collector everywhere meets females recently matured or in late stages, and males of the same ages in almost equal numbers. By late summer males and females are to be found living in the same webs, few of which now contain egg-sacs. Apparently the mature females met in summer are the immatures of the previous fall. After the cycle of maternal functions is completed, they die out, which explains the scarcity of adult females as fall approaches. Ordinarily the life cycle appears to be a little over a year, but this probably varies according to environmental factors.

We have witnessed the actual mating on three different occasions. The first was between a female which only the day

before had completed her final molt, and a male which, because of his size and light color, was thought to have several stages yet to go to maturity. As the mating of spiders has not often been observed, and that of the black widow in particular has not been recorded before, so far as we know, we shall describe the occurrence in some detail.

On the morning of August 11th one of us (W. V. R.) observed a web across the mouth of a large hole in a bank of the Platte River. The web was found to contain three males and a large female. No egg-sacs were present. During the course of the day courtship between one of the males (the largest of the three, although his coloring was not that of a mature male) was observed. At long intervals he slowly approached the female, waving his forelegs and, when near, he tentatively stroked her. She responded by exhibiting great anger, shaking the web and lunging at her suitor, who made off rapidly. She made no effort to pursue him; he, in his turn, occasionally chased the other males away, in a mild, half-hearted manner. Once he rested for twenty minutes with the tip of one foreleg touching the tip of hers. Suddenly she jumped at him and seized him and could easily have destroyed him had her hostility been real.

The observer returned that night, thinking that with creatures reputed to be nocturnal, events might progress more rapidly then. Fabre states that the only mating he ever witnessed took place at night. However, the flashlight seemed to disturb the female who kept out of sight most of the time.

On returning the next morning, it was found that one of the males was missing. The chief characters, however, were still engaged in courtship, the female seeming more willing to permit the advances of the male, although too great a degree of intimacy was still resented. This continued throughout the day. It being no longer possible to continue the observations in situ, the specimens were captured and placed in bottles in the laboratory. The female was left alone for several days to become accustomed to her new home. One morning it was found that she had eaten a beetle and also undergone a molt. This last may be of significance if it be true that sexual maturity is not reached until the final molt. The male was now introduced. Within a few hours he recommenced his advances and this time she appeared willing to permit them. She hung motionless in her web, abdomen up, the male excitedly crawling all over her. There followed periods of quiet, the male occasionally coming to rest close to the female. At such times it was noted that his abdomen vibrated with great rapidity. The vibrations are necessarily transmitted to the female by means of the web and perhaps serve to excite the female sexually or notify her of the presence of a lover. Finally, after repeated maneuvers of this sort, the male again approached the female and came to rest upon her abdomen, his head at the level of her epigynum, the tips of their abdomens even. The female remained motionless and apparently indifferent. Fecundation then took place, the male inserting first the intromittent organs of the right pedipalp, his body shifted somewhat to the left. Contact was continued for fifteen minutes. He then retreated momentarily, then returned and, with body shifted to the right, introduced the organ of the left pedipalp for a period of ten minutes. He then retreated, wiping the pedipalpi with his forelegs. The female followed him. He ventured a parting caress only to be struck at viciously.

For the next few days the pair was

closely observed. Traditionally the female should kill the male immediately or at least very soon after mating. They were well supplied with grasshoppers and beetles, of which both partook. Finally, after ten days, the lifeless body of the male was found hanging in the web. She certainly may have killed him, although there are reasons for doubt. First of all, he had shown himself throughout equally as agile, perhaps more so than she, and had had no difficulty avoiding her previously. Furthermore, the other male taken from the same web and kept alone was found dead a day later and a third male, collected elsewhere, died within the week. All the males that we have attempted to keep in captivity have lasted but a few months at best and this fact, coupled with the observation that males become very rare in the middle of the summer and are only plentiful in spring and fall, leads us to think that the life cycle of the male is considerably shorter than that of the female. Thus it seems quite possible that the widow may be a relict, not as a result of her own criminal propensities, but from natural causes alone.

The mating just described took place on August 18. The female was kept in a quart specimen jar and fed on grasshoppers and beetles, later on meal worms, then was transferred to a milk bottle containing an ordinary fruit fly culture and stoppered with a wad of cotton, this being an easy and successful way of wintering these spiders. In the spring she was put back in the specimen jar and fed meal worms and angle worms. Not until July 12 did she produce her egg-sac. This produced spiderlings in the normal way within the next month, and not long after she was dead. She was being fed on angle worms at this time and, as a number of other deaths occurred within a short period, we came to the conclusion that these worms may not be a suitable diet. In contrast to this female, which carried the sperm to fertilize her eggs just one month short of a year, another which was observed to mate on June 11, 1935, produced an egg-sac on July 6. We have also had a female which produced three egg-sacs from none of which spiderlings emerged, only to be followed by a fourth with a normal emergence. The third mating, which occurred on August 14, 1935, involved a female which had occupied a web in the garage of a friend for the entire summer and a male which appeared suddenly only a day before the mating occurred. Very careful notes of the proceedings were kept by Mrs. F. W. Miller, to whom our thanks are due. The mating required nearly three hours, the details being much as described above. The sequel, however, was quite different. Upon completion the partners withdrew some distance, with, however, no signs of hostility, and occupied the same position the last time they were inspected that evening, at about 11:00 p.m. The next morning, however, to our great astonishment, we found the female dead, and the male feeding upon her. There was no sign of any accident, the web had not been disturbed. Whether he had killed her or not we do not know. But she was dead, he was alive and was eating her, the ancient tradition to the contrary notwithstanding.

Development

Many of our females produced from one to four egg-sacs in captivity. The process probably generally takes place at night, but was several times observed in the laboratory during the day. We found an average of 143 eggs in ten sacs, the maximum being 210. The eggs are whitish, smaller than the head of a common pin,

and covered with a sticky substance. The egg-sac mentioned above as being produced on July 6 was started at 8:40 in the morning. This female was confined in a square glass case about eight inches high and six across. She had previously settled on one of the upper corners for her nest which was merely a roughly funnel-shaped thickening of the web. Working, as always, from below, she first spun a shallow disk about a half-inch in diameter. Against this she pumped up a sticky, yellowish mass of eggs, pausing to rest from time to time. At 9:10 she was spinning a blanket around the eggs. We quote from our notes:

> Two or three threads coming from spinnerets. She touches fabric with spinnerets, then draws away and handles threads with hind legs (these have the "combs"), then turns a little and does it again, making a very loose cottony felt all around ball of eggs. Color, white. That of egg mass, yellow. She is not disturbed by being moved. The egg mass can be seen in the center through the wall of felting. Egg ball about $\frac{3}{4}$ inch in diameter. Felting $\frac{1}{16}$ inch thick. Now 9:20. She is going over the surface, touches with spinnerets, then another spot close by. Not using legs to handle silk. The beat is 2 per second. This is evidently making outer coat. It is more yellowish than felt, but not as yellow as mass of eggs. She does not use her hind legs at all in this process. Just tap, tap, tap with spinnerets. Makes a fine fabric that quickly gets opaque. At 9:55 it is finished.

In nature the egg-sac is held in the web by stay lines, but may be moved with considerable facility. When the web is disturbed the spider quickly hauls the sac back as far as possible out of danger. When the sun is shining and nothing threatens, the sac is hung near the mouth of the web. Temperature and humidity are possible factors influencing the time of emergence, which is ordinarily from two to three weeks. Hatching from the eggs apparently may take place within a few days, but the young do not emerge for a varying length of time. From the fact that the magnifying glass shows casts in the debris of the emptied egg-sac, it appears that the young make their first molt before escaping. Considering the minute size of the prisoners and the toughness of their confining walls, the problem of escaping must be a serious one. However, two or three pin-holes are eventually made in the sac and the spiderlings swarm out.

We have not succeeded in inducing the young to feed except upon each other, which may be their habit in nature. We doubt, however, that cannibalism begins while the spiderlings are still confined in the egg-sac. Many empty egg-sacs have been examined in our search for parasites and in the sac from which a normal emergence has occurred we usually find only casts and egg membranes, rarely a dead spiderling. Three egg-sacs produced at intervals by the same female were allowed to hatch in a single container. The older and stronger fed on the younger and upon each other till at the end of the summer only three, all females, had survived to approach maturity.

According to Lawson (5), eight molts take place before maturity, the ninth instar representing the adult stage. Food supply and environmental factors influence the time between molts, which is usually from 9 to 18 days. Under favorable conditions full development requires 2 to 3 months, sometimes longer.

Appearance

Progressively through the instars the specimens show changes in pattern and color. The characteristic markings are really beautiful. At all stages in both male and female the telltale hourglass may be identified on the ventral side of the abdomen, though it varies much in color. Lawson gives a detailed account of the appearance of the female in each instar. As we observed it, the basic color of the

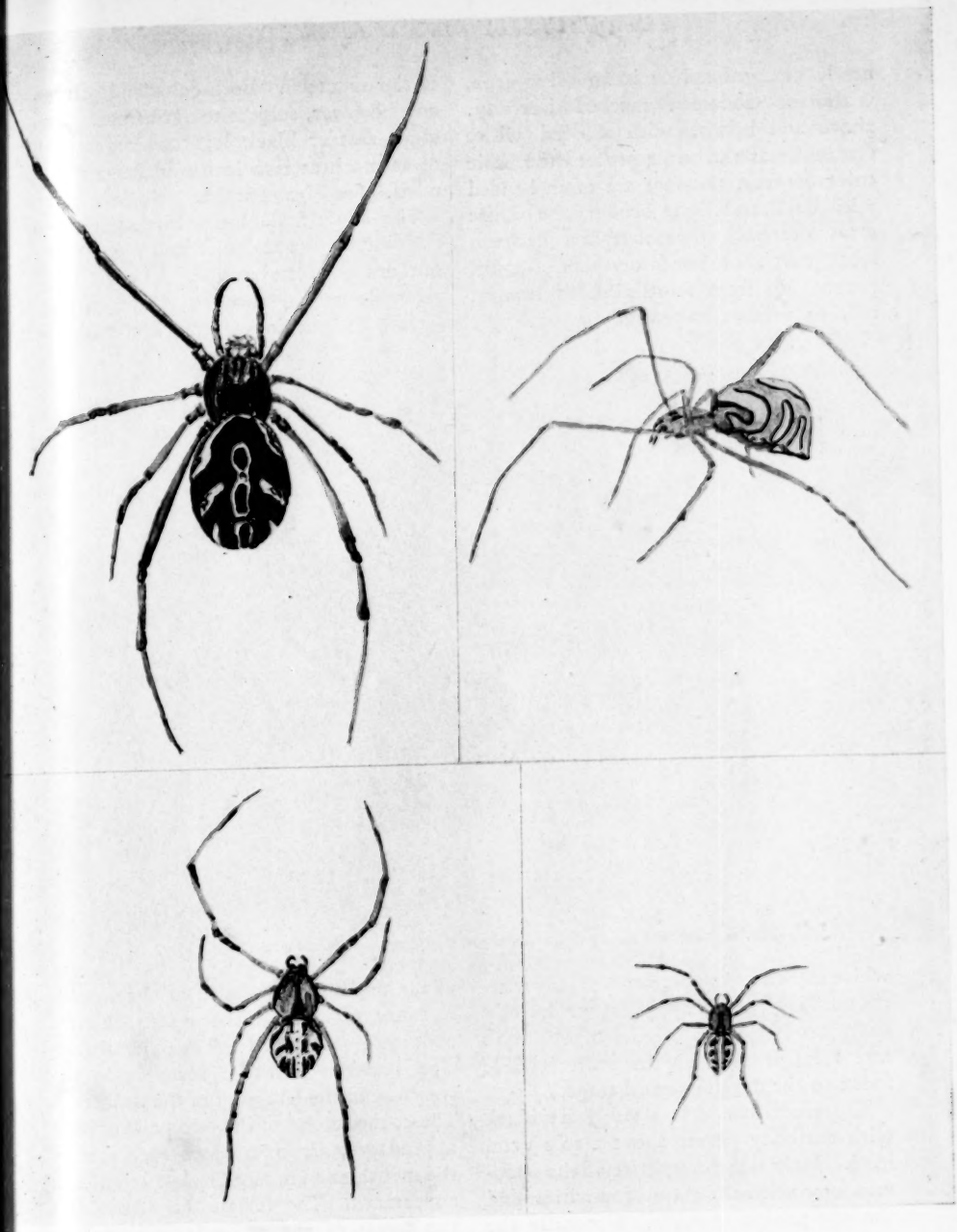

FIG. 1. FOUR STAGES IN THE DEVELOPMENT OF THE FEMALE

About two molt intervals. The largest is about two molts removed from maturity, the smallest is the spider as it emerges from the egg sac. × 6.

newly emerged spider is an olive drab, with the abdomen marked liberally. above and below, with a dead white Gradually as the molts proceed the basic color darkens, the legs are often banded with dark and light brown, the white areas decrease, the hourglass becomes more prominent, bands or spots of color, progressing from faint pink to orange, red, or yellow, appear along with the of the abdomen. Both color and pattern are, however, subject to variations. The eight slender black legs cover a spread of as much as two inches in large specimens. See Figs. 1 and 2.

The adult male has white stripes on the sides of the abdomen and a conspicuous orange dorsal stripe. It bears considerable resemblance to the immature female at certain stages. The male is

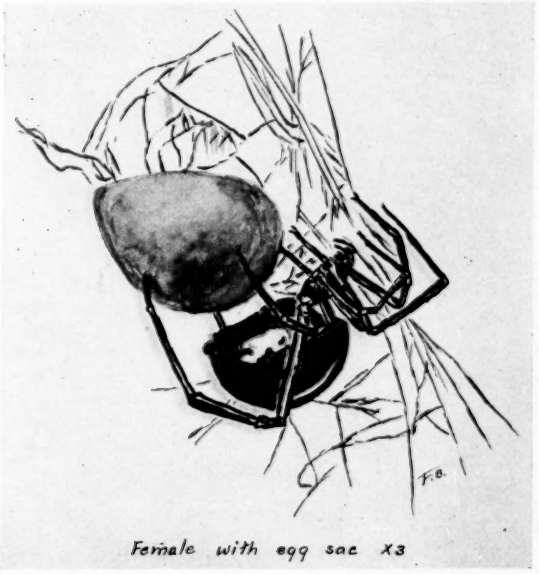

FIG. 2. MATURE FEMALE IN CHARACTERISTIC POSITION GUARDING EGG SAC. × 3.

white markings on the back. These latter markings generally disappear entirely with the last molt. The length of the fore tibia is used as the most reliable index to the developmental stage.

The adult female is a shiny jet black with the body proper about 1 to 1½ cm. long. Body weight and size of the abdomen vary with the state of nutrition and the egg producing cycle. Generally the body is entirely black except for the orange-red hourglass on the ventral side about one-fourth the size of the female, and has a slender rather than spherical abdomen. See Fig. 3. The chief distinction between the two sexes is in the structure of the last joint of the pedipalps. These, the second of the two pairs of head appendages, are situated on each side of the mouth and are more or less leg-like in appearance. The female *Latrodectus* has the tarsus of the pedipalp ending in a single claw, as is true of the females of many genera. During the third instar of

the male the pedipalps show signs of enlargement, which progresses during the fourth and fifth instars. In the final molt complex intromittent organs are produced as bulblike structures on the ends of the pedipalps. They have no direct connection with either testes or vasa deferentia. The seminal fluid produced in the gonads of the abdomen is deposited upon a delicate web which the male spins. This fluid is then taken up by the specialized genital appendage of the palpus, by which it is transferred to the female at mating.

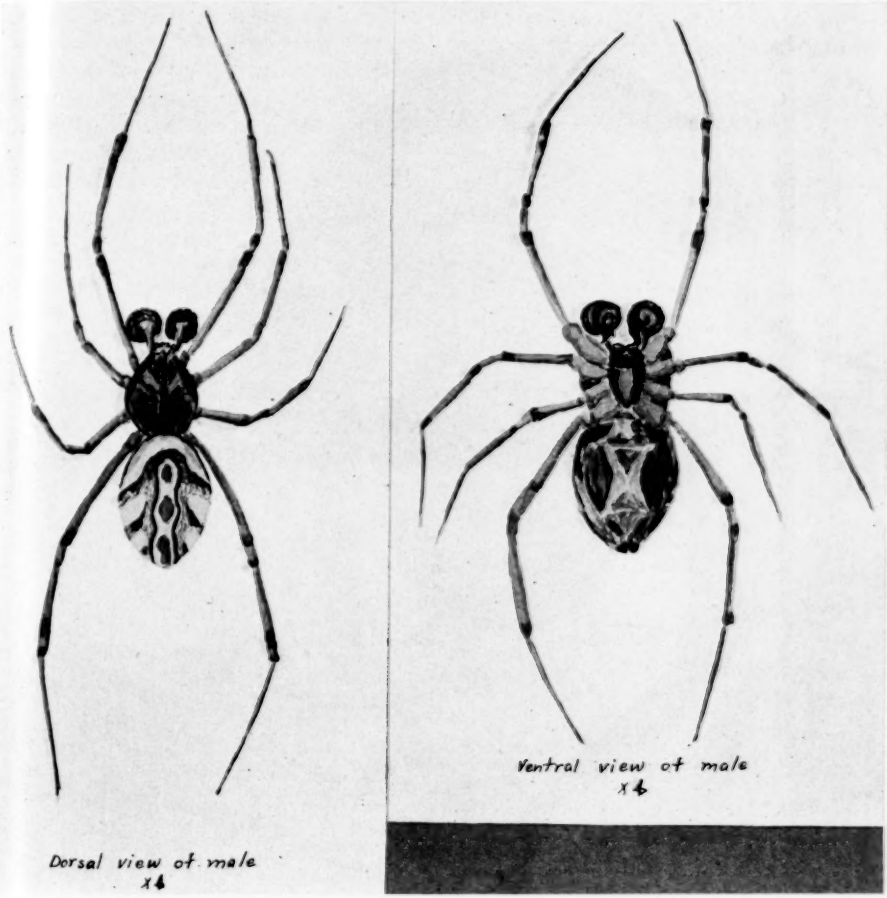

FIG. 3. MALE. PROBABLY MATURE, AT LEAST WAS CAPABLE OF FERTILIZATION
Left—dorsal view. Right—ventral view. × 6

The cephalothorax of the adult female seems to vary in proportion to the general size of the animal and the length of the appendages. It is somewhat shield-shaped, with four shallow acetabula on

each side to receive the coxae of the legs. See Fig. 4. The dorsal anterior angle composes the median ocular area, on which are located the eyes in two rows of four each. Beneath the eyes and

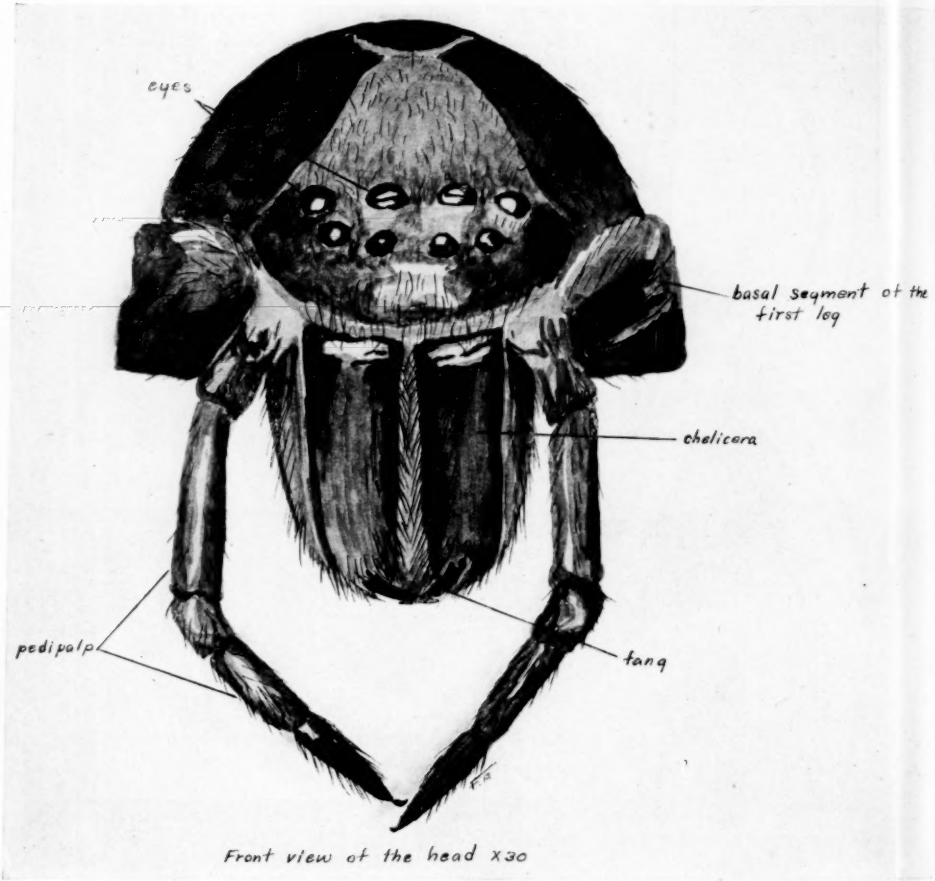

FIG. 4. DIAGRAMMATIC, ANTERIOR VIEW OF HEAD, SHOWING CHELICERAE AND FANGS OF MATURE FEMALE

of insects. They are situated in front of and above the mouth. Invariably they are made up of two joints, the proximal paturon or tige, and the distal unguis or fang. The paturon is stout and conical

separating them from the first pair of appendages is a sclerite called the clypeus. The first appendages, or chelicerae, are homologous with the second antennae of crustaceans, and not with the mandibles and well provided with stiff hairs. The unguis is a reddish brown, sickle-shaped claw of hard chitin. The chelicerae are articulated so that their principal motion is lateral with the two fangs directed

toward each other in action. The mouth is fitted for the taking of liquid food only. When the victim has been sucked dry, the hard parts are discarded. On the top of the cephalothorax just behind the ocular area is a smooth triangle set off by shallow grooves. Beneath this triangle and the ocular area lie the pair of poison sacs. Slender ducts lead through the hollow chelicerae and fangs to a mesial aperture close to the tip of the claw. It was found that the glands could easily be removed by a procedure described in detail later.

The glands are white, often curved, sacs, varying from 1 to 2.5 mm. in length, and generally about 1 mm. thick. The weight varies from 1.5 to 2 mg. The wall is surprisingly tough. The outer wall of the sac is made up of strong muscle fibers. Beneath the muscle layer is a thin sheath of connective tissue, supporting the secretory cells which project into the lumen of the gland. They appear to be columnar and arranged in a single row with the nuclei toward the bases of the cells. See Fig. 5. The cytological processes involved in the production of venom have not been worked out.

The poison glands of the male are in the same location as in the female, and of the same general appearance, but proportionately smaller. The male does kill small insects for food, but whether or not by the use of poison could not be ascertained.

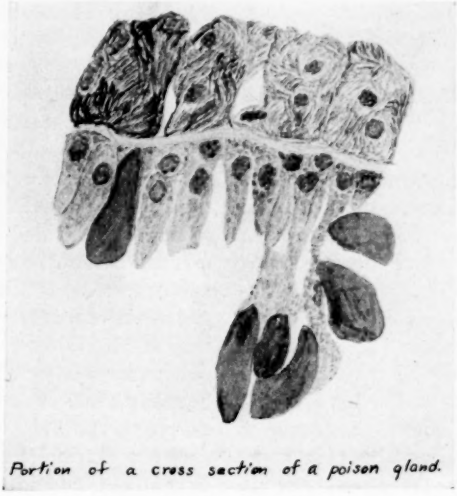

FIG. 5. HISTOLOGIC SECTION OF VENOM GLAND
The masses represent secretion precipitated by fixing agent. Hemotoxylin and eosin stain.

Means of Dispersal

Spiders show two definite tropisms. When they are young they are negatively geotropic, tending to climb upwards; at all stages they are negatively heliotropic, tending to move away from the light. The geotropism of the young provides a means of dispersal. Once the maiden flight has been effected and dispersal accomplished, the spiders no longer exhibit the tropism. The following ob-

servations on the dispersal of the spiderlings were made by us.

A glass tube about an inch and a quarter in diameter and three feet long, enclosing a piece of bamboo of the same length wound with raffia, was closed with cloth at both ends after a newly made egg-sac had been placed inside on the bottom cloth. The whole contrivance was then set upright in a retort stand. The bamboo inside the glass tube would furnish the spiderlings something to climb on should they have the instinct to do so after emergence from the sac. About four weeks after the spinning of the sac, there were two little swarms of fifty or sixty spiderlings each at the base of the tube near the sac. During the day they all climbed their artificial tree and swarmed at the top of the tube. The next morning the apparatus was carried out into the country, the top cover removed, and the length of the artificial tree increased by a three-foot stick. Immediately about fifteen of the little spiders detached themselves from the swarm and intently climbed to the very tip of the new stick. The sun was shining and a little breeze blowing from the south. Suddenly a tiny mite was snapping about in space eighteen inches or two feet from the stick. It was a spiderling waving in the breeze at the end of a gossamer drag-line which it had spun as it was blown from its moorings. Then the spider was observed to be working its way back along the line, not drawing in the line but leaving it out, possibly doubling it. The adventurer reached his dock again, leaving the silken thread flapping in the breeze. Suddenly the line broke at its base, or was cut by the spiderling behind him, and he sailed away into space too rapidly for the eye to follow the course very far. This happened again and again, till of the original fifteen adventurers only two or three remained. This explains the disappearance of the young spiders from the maternal web so soon after emergence, and explains also their being found later in life in curious places to which chance blew them on their initial flight.

When the young spider ends its voyage, we must imagine that it seeks the first hole or crack available as shelter. Here it spins a web not unlike that of the mother, but on a small scale, catches its prey in the same way, and if circumstances are propitious, sets up a permanent establishment.

Enemies

In spite of the fact that the poison of the widow is deadly to all small animals, she has a number of natural enemies. We have observed the vireo feeding the spider to her nestlings and pigeons and chickens may eat it with impunity, the latter with apparent relish. Field mice and related mammals probably take the spider when they find her, since we have never observed one under a rock that shelters rodents. Possibly some of the hunting spiders can overcome the widow, although in laboratory observation she has always prevailed over any other spider put in with her.

Newspaper items from time to time report discoveries of what we judge to be parasitic wasps and ichneumon flies designed to exterminate the black widow. Our observations indicate that she, when full-grown, can handle any wasp that might attack her directly. We have found, in the debris of the spider's web, in the empty egg-sacs and in various other similar places the active and omniverous larvae of one of the Dermestid beetles, the common museum pests. Whether these grubs are only scavengers cleaning up the waste from the spider's table, or

are also capable of destroying the living eggs, we have not been able to determine as yet. But we suspect that both are true.

There can be no question, however, but that the blue mud dauber (*Chalybion cyaneum*, Klug) is a predator on the black widow. We have collected many mud dauber nests and have frequently found immature black widows stored as food for the larvae. Recently Irving and Hinman (6) have published similar findings. In Lamar, Colorado, where black widows have been extremely prevalent the past two years, residents have told us that the mud daubers seem unusually scarce. It may be that in nature the mud dauber is one of the chief factors in holding the black widow in check.

EXPERIMENTAL

Studies on Toxicity

The first problem was to study the toxicity of the venom and to develop a reliable means of assay. Most experimental studies previously reported fall under two heads as far as the source of the material used is concerned. Some workers have proceeded by placing the spider upon a shaved area of the animal used and pinching it with forceps until it bit. Others have used the macerated heads of the spiders as their experimental material. Early in our work we tried both methods, but soon learned that they were unreliable and that consistent results could not be obtained. If one employs the first technic, he encounters several factors which are difficult or impossible to control. The actual amount of venom introduced will obviously be dependent upon the size of the spider, its past history, (that is, how long since it last made use of its poison apparatus and the speed of regeneration of the poison), and upon the degree of anger aroused by the pinching. As will be shown later, even under conditions which one might suppose would excite the greatest degree of anger, that is, after victory in mortal combat with another spider, the glands still contain a considerable amount of venom. It seems likely that the glands are under some degree of volitional control and the amount ejected will depend upon the degree of irritation of the spider. This is supported by the experience of Baerg (7) who speaks of spiders which bit readily and caused severe symptoms while others attacked only under extreme provocation.

TABLE 1

WEIGHT OF RAT	SPIDER	RESULTS
264	Large	No symptoms.
280	"	Comatose all afternoon and night, breathing shallow, hind legs paralyzed. Recovered.
308	Small	Symptoms much like above, in addition, foreleg paralyzed, large swollen area at site of bite. Recovered.
65	Average	Severe paralysis in all legs. Could not use legs, could be slid across table. Breathing became difficult, died after 48 hours.
73	"	No symptoms.
80	"	Slight paralysis, recovered.

As for the second method, that of using macerated heads as a source of material, if a sufficiently large number of spiders is used, the size and past history factors are averaged and, of course, the question of degree of irritation does not enter. However, anyone who has ever dissected out the venom glands will have noted their toughness and elasticity. Macerating the heads, even though the operation

is carried out thoroughly, will certainly fail to crush all glands. An unknown number will escape maceration and will then be discarded with the debris. The following tables illustrate the above points. Table 1 gives the results of actual biting experiments. In these trials spiders were used which had been kept in the laboratory three days and had not been fed during that period. These were placed upon shaved areas of the rat's abdomen and excited to bite by being pinched with forceps. The results are seen to be very inconsistent.

In Table 2 the results of two experiments are shown in which macerated heads were used, 40 heads being used in each batch.

TABLE 2

BATCH	NO. OF RATS INJECTED	AMOUNT INJECTED	PER CENT DEAD
1	10	Equiv. 2 spiders	70
1	10	" 1 spider	10
2	10	" 2 spiders	0
2	10	" 1 spider	0

The wide variation in effect no doubt indicates failure to crush and extract all glands.

Comparison of these results with the toxicity curve for venom obtained later indicates that even in the more active preparation a large number of glands must have escaped extraction.

In view of the inconsistent results shown above we adopted the following procedure as a routine method in the preparation of all venom used in the succeeding experiments. No fewer than 20 spiders, in some cases as many as 80 spiders were used in the preparation of each batch of material and in this way individual differences were averaged. The spiders were placed under light chloroform anesthesia, the abdomen clipped off and the cephalothorax and legs imbedded in molten paraffin on a microscope slide. Solidification of the paraffin held the spider in a firm mounting. Under the dissecting microscope the skin of the head above the eyes was clipped off; the venom glands were then clearly visible and could be removed with fine forceps. The glands were then placed in physiological salt solution and carefully pulled apart and thoroughly macerated. The glandular debris was transferred to fresh saline, again macerated and washed and discarded. The washings were added to the original solution.

Young rats, fifty to sixty grams in weight, were chosen as test animals, first, because of their availability in this laboratory and second, because preliminary experiments showed that they were quite susceptible. A relatively small amount of venom would cause death and an adequate amount would produce a chain of symptoms which was a very definite and constant one.

The Toxicity Curve. The work of Trevan (8) on biologic assays in general and the work of Coward and Burn (9) and ourselves (10) on the assay of estrin preparations has clearly indicated the necessity of using large numbers of animals in the assay of biologic preparations in order to overcome the individual variation which exists between animals of the same species, weight and age. In order to establish the toxicity of spider venom we therefore injected varying amounts into groups of ten rats per dose. Fig. 6 shows the results obtained, with the amount of venom indicated both in fractional parts per spider and in absolute weight.

As will be noted, the average lethal dose, that is, the amount of venom which will kill fifty per cent of the rats, is one-fourth the venom contained in the glands of one spider, or .032 mg. This is the

amount meant when the term "Average Lethal Dose" or "Equivalent of one-fourth spider" is used in describing subsequent experiments.

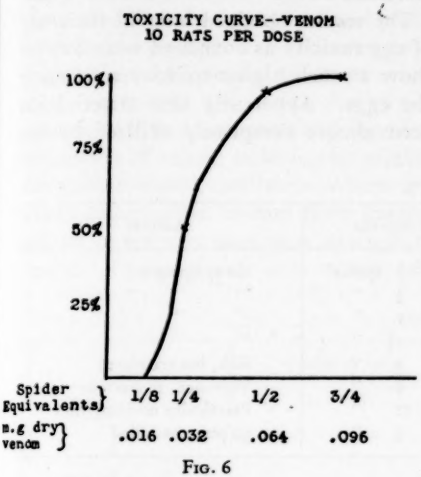

FIG. 6

Mode of Injection. In obtaining the above toxicity curve, as well as in practically all of the later work, intraperitoneal injections were given. A preliminary study, the results of which are shown below, indicated this type of injection to be preferable inasmuch as the amount of venom necessary to cause death was somewhat less and also the length of time before death occurred was shorter when intraperitoneal injections were given. As we did not know in advance how plentiful the spiders would be, we naturally made use of the method which would require the least expenditure of venom, and having used this method in obtaining the toxicity curve continued with it in further experiments so that the results would be comparable.

Weight of Rats. The weight of the rat is an important factor in the amount of venom necessary to obtain a required result. For reasons given, we used immature rats weighing between 50 and 60 grams. Litters in prospect promised an adequate supply of rats of this size throughout the summer months. No extensive experiment was carried out to discover the ratio of venom to body weight; however, Table 4 gives the data on the few trials which were made.

Type of Spider. The spiders used throughout in the work reported elsewhere in this paper were mature females as indicated by the absence of any markings on the dorsal surface. See Plates. However, it seemed desirable to investigate the toxicity of immature females and of males as well. For this purpose glands

TABLE 3

TYPE OF INJECTION	NO. OF RATS	AMOUNT INJECTED	PER CENT DEAD	MAX. LIFE
Subcutaneous	5	Equiv. $\frac{1}{4}$ spider	0	———
"	5	" $\frac{1}{2}$ "	60	36 hours
"	5	" 1 "	100	24 "
Intraperitoneal	10	" $\frac{1}{4}$ "	50	12 "
"	10	" $\frac{1}{2}$ "	90	8 "
"	10	" 1 "	100	8 "

TABLE 4

NUMBER OF RATS	WEIGHT	AMOUNT INJECTED	PER CENT KILLED
10	50–60 gm.	Equiv. $\frac{1}{2}$ spider	90
4	100–150 "	" 1 "	50
12	200–250 "	" 1 "	33
8	200–250 "	" 2 spiders	100

from both groups were obtained in the usual way and injected. The results are given in Table 5.

These results indicate that the difference in toxicity is qualitative as well as quantitative.

Toxicity of Baby Spiders. As stated in the section devoted to natural history, the eggs hatch within the egg-sac and there the spiderlings undergo their first molt. It seemed interesting to compare the toxicity of the baby spiders with the eggs from which they came, therefore spiders 7 to 10 days after their emergence from the egg-sac were studied, as it was thought that much of the material from the egg would by that time have been utilized. Since it was impossible to dissect out the glands, the spiders were macerated in saline, the debris filtered off, washed in fresh saline and the washings added. Undoubtedly many of the venom glands would not be crushed in this process and the toxicity indicated in Table 6 resides in the tissue fluids of the spiders and possibly in unabsorbed egg material.

The results obtained later in the study of egg toxicity as compared with Table 6 show a much higher toxicity residing in the eggs. Apparently this material has been almost completely utilized by the time the young spiders reach the age of one week.

Degree of Exhaustion following Biting. As previously mentioned, other workers have studied the toxic effects of the venom by causing spiders to bite their victims. Among others, Baerg (7) describes experiments done upon rats in which the first bite resulted in severe symptoms, a subsequent bite in less severe symptoms and the third in no symptoms whatever, from which he concludes that immunization

TABLE 5

TYPE OF SPIDER	NO. OF RATS	AMOUNT INJECTED	RESULTS
Immature Females	3	Equiv. $\frac{1}{4}$ spider	No symptoms
" "	3	" $\frac{1}{2}$ "	" "
" "	3	" 1 "	" "
" "	2	" $1\frac{1}{2}$ "	" "
" "	3	" 3 "	Sick, but recovered
" "	2	" 6 "	Very sick, recovered
Mature Males	1	" 12 "	Practically no symptoms
Mature Females	10	" $\frac{1}{4}$ "	50 per cent killed

Average Length of Venom Glands, Mature Females..... 1.75 mm.
" " " " " Immature Females..... .75 mm.
" " " " " Mature Males..... .75 mm.

TABLE 6

NUMBER OF RATS	AMOUNT INJECTED	RESULTS
5	Equiv. 1 spider	Slight paralysis, recovered
2	" $2\frac{1}{2}$ "	" " "
2	" 5 "	Severe paralysis, recovered
2	" 10 "	One died, other very sick, recovered

had occurred. As will be shown later, immunization develops much more slowly than these results would lead one to believe. In experiments done upon himself, Baerg obtained almost opposite results, the first bite causing only local pain, whereas the second was followed by a very serious and painful chain of symptoms.

We tested the question of the degree of exhaustion of venom in biting by placing the spiders under conditions where one would expect them to bite their hardest and to inject the maximum amount of venom. These spiders are notoriously cannibalistic. It is a well known fact and one which we have observed repeatedly, that when two mature females, especially if one is attending an egg-sac, are placed in one container, they will fight furiously until one or the other has been bitten and killed. We placed spiders together under these conditions; in the first experiment the victor of one match was matched with another victor; in the second, spiders were used which had only bitten once. The results are shown in Table 7.

TABLE 7

	NUMBER OF RATS	AMOUNT INJECTED	RESULTS
Experiment 1	1	Equiv. 1 spider	Died
" 1	2	" ½ "	Sick, recovered
" 2	1	" 1 "	Died
" 2	2	" ½ "	Sick, recovered

The spiders in experiment 1 had bitten others twice within a half-hour before being killed, those in experiment 2 had bitten others once within a half-hour before being killed. These results show that the glands still contain a considerable amount of venom—at least one-fourth the total amount—even after the spider has used them twice within the previous half-hour. It should also be stated that, where the spider was biting for the second time, the victim usually recovered. No experiments were carried out to determine the length of time necessary for regeneration of venom.

Potency of Venom in Terms of Weight. The poison glands were removed from twenty spiders and dried in air for twelve hours. They were then weighed. Following thorough maceration in distilled water the glandular debris was dried and weighed. The difference between the two weights is taken to represent the dry weight of the venom. This is not entirely correct, since unavoidably some glandular elements were lost in maceration. The figure obtained errs, therefore on the side of assigning a somewhat lower potency to the venom than is actually the case. Table 8 shows the results.

TABLE 8

Dry weight of glands from 20 spiders	4.0 mg.
Dry weight of debris	1.48 mg.
Dry weight of venom	2.52 mg.
Dry weight of venom per spider	.126 mg.
Dry weight per A.L.D.	.032 mg.

These results indicate that on the basis of weight the venom of the black widow is extremely potent. In man, the spider bite results fatally in about five per cent of all cases (Bogen, 2). The rattlesnake is said to kill in from 15 to 25 per cent; the actual amount of venom introduced is, however, much greater in the case of the snake. Experimentally, Calmette found

that .2 mg. of cobra venom will kill a guinea pig, and Noguchi states that 5 mg. of rattlesnake venom will kill a 350-gram guinea pig in 24 hours. The following comparison of the potency of black widow with rattlesnake venom was made. Two specimens of the common prairie rattlesnake, (*Crotalus albicans*, Say) were collected, one a male three feet long with 8 rattles and the other a female two and one-half feet long with 6 rattles. The venom was obtained by pressing upon the glands, then dissecting them out and washing with distilled water and evaporating to dryness. 32 mg. of dried venom were obtained from the large snake and 20 mg. from the small. The venoms were pooled and assayed. The results are given in Table 8a.

TABLE 8a

NUMBER OF RATS	AMOUNT INJECTED	PER CENT KILLED
10	.75 mg.	0
10	1.0	90
10	1.5	100

As .064 mg. of spider venom killed 90 per cent of injected rats, it appears to be about 15 times as potent on a dry weight basis.

Comparison of Colorado and California Spiders. Through the kindness of Doctor Emil Bogen, of Olive View, California, we were able to compare the toxicity of spiders from that region with Colorado spiders. Nine mature females were received which resembled our local spiders in every way but were somewhat smaller. The venom was obtained in the usual manner. The results are given in Table 9.

This seems to show a higher degree of potency for the local spiders. However, our assay was made on spiders collected during July; the Californians were collected in October, so a seasonal variation may be indicated.

Toxicity Studies on Eggs. A large amount of work has been done upon the hemolytic principle or arachnolysin of eggs, particularly by Levy (11). This poisonous material is found in the tissue fluids of all spiders, and reaches its highest concentration in their eggs. It appears to be fairly well established that the nature of this substance differs both in its chemistry and its effects from the venom. Since we intended to do some work on this question, particularly cross-immunization experiments, it seemed desirable to prepare a toxicity curve for eggs as well. This curve is shown in Fig. 7.

TABLE 9

	NO. OF RATS	AMOUNT INJECTED	PER CENT KILLED
Colorado spiders	10	Equiv. $\frac{1}{4}$ spider	50
" "	10	" $\frac{1}{2}$ "	90
" "	10	" $\frac{3}{4}$ "	100
California spiders	8	" $\frac{1}{4}$ "	25
" "	6	" $\frac{1}{2}$ "	33
" "	4	" 1 "	75

The dry weight of the egg poison was determined by macerating a weighed and counted sample of eggs, obtained from 10 different egg-sacs, in distilled water. The poisonous principle is apparently either a globulin or associated with globulins, as it is insoluble in distilled water but is soluble in dilute salt solutions. The solution was allowed to stand overnight

in the refrigerator and was then filtered. Upon drying, the precipitate is pale yellow and flaky in texture. The averages of several experiments, in which samples were taken from 5 to 10 different egg-sacs, show that 1,000 eggs weigh 640 mg., and yield 100 mg. of dried precipitate. It should be pointed out that the figures in the above graph indicating dry weight were not obtained by actual injection of dried material, but were obtained by calculation. The actual injection of dried material shows a considerable loss of potency as a result of chemical manipulation or as a result of drying. This point is illustrated in Table 10.

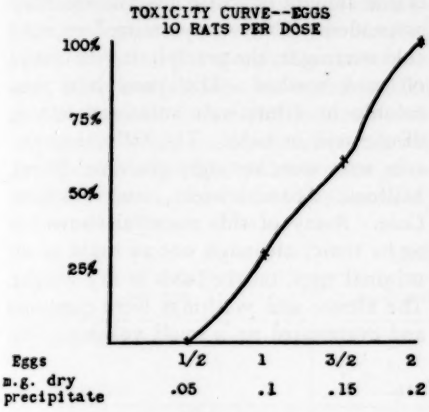

FIG. 7

TABLE 10

MATERIAL INJECTED	NO. OF RATS	EQUIVALENT OF DRY MATERIAL	RESULTS
Fresh eggs	10	.1 mg.	30 per cent killed
" "	10	.15	60 " " "
" "	10	.2	100 " " "
Dried Ppt.	4	.1	0 " " "
" "	4	.25	50 " " "
" "	4	.5	100 " " "

A comparison of the toxicity of black widow eggs with the eggs of the common brown house spider was made and indicated a much higher degree of toxicity resident in the black widow eggs. In both cases eggs were taken from ten different sacs and pooled. The results are shown in Table 11.

TABLE 11

SOURCE OF EGGS	NUMBER OF RATS	NUMBER OF EGGS INJECTED	PER CENT KILLED
Black Widow	10	1	30
" "	10	2	100
Common Brown	5	3	0
" "	3	7½	0
" "	3	15	100

Keeping Qualities of the Venom and Eggs. Various zoologists and popular writers on the black widow make mention of the fact that certain aboriginal tribes make use of both the venom and of the poison contained in the eggs to tip their arrows. Also it may become important in the gathering of venom for experimental purposes and in the preparation of serum, to know whether desiccation is resisted. On the third of July ten spider glands were macerated in a dry evaporating dish, covered with gauze and set aside at room temperature until August 23rd, when saline was added, the venom dissolved and assayed. Forty eggs were handled in a similar fashion. Table 12 shows the results of the assay. These results indicate that there is little, if any, loss in

potency as a result of drying for a period of 7 weeks.

Venom dissolved in saline and allowed to stand at room temperature without preservatives for the same length of time had lost all potency. We did not study the effect of preservatives over long periods of time, but did determine that solutions made up either in 10% glycerin or in 1:1000 merthiolate did not lose potency when stored for a period of one week.

Chemistry

Chemistry of Egg Poison. The very thorough work of Levy (11) on arachnolysins has elucidated many points of interest in regard to these substances. He, and others, believe them to be elaborated by all spiders, and present in all tissue fluids, reaching their highest concentration in the eggs and legs, and there is considerable evidence supporting the view that this poison is not identical with the venom. Our studies were directed mainly to this question which we attempted to solve by cross-immunization experiments. Some observations concerning the chemistry were made, however, and are reported here.

Exp. 1. A weighed quantity of the eggs were macerated in saline solution. This solution was neutral to litmus. Thorough extraction with ether yielded, in the ether fraction, a small amount (less than 1%) of a yellow oil, which, emulsified in water and injected, was shown to be inert. Subsequent ether extractions of the egg solution made acid (.1%) with HCl or alkaline with NaOH (.1%) removed nothing.

Exp. 2. Macerations of eggs in distilled water gave a solution in which a considerable amount of white material remained suspended. This was permitted to stand cold overnight, the precipitate was filtered off and washed. The precipitate was soluble in dilute salt solutions and in dilute acid or base. The following protein tests were strongly positive: Biuret, Millons, Adamkiewiecz, and Hopkins-Cole. Assay of this material showed it to be toxic, although not as toxic as the original eggs, on the basis of dry weight. The filtrate and washings were combined and evaporated to a small volume. Protein tests gave a weakly positive Biuret and Millon test. The assay resulted negatively in the amounts used. The results are shown in Table 13.

TABLE 12

MATERIAL	NUMBER OF RATS	AMOUNT INJECTED	RESULTS
Venom	2	Equiv. of 1 spider	All killed
"	4	" " ½ "	" "
Eggs	2	" " 4 eggs	" "
"	4	" " 2 "	" "

From the above data it may be assumed that the toxic material found in the eggs is neither a lipoid nor an alkaloid, but is probably a globulin or associated with globulins.

Chemistry of Venom. When venom glands are macerated in distilled water, a cloudy, opalescent solution is formed which is neutral to litmus. Standing in the cold causes a small amount of white precipitate to settle out. This precipitate is toxic, but accounts for only a small portion of the total toxicity. The precipitate gives the usual tests for protein and is soluble in dilute salt solutions. It

is our belief that it represents a globulin similar to, if not identical with that found in the eggs and is a contamination from the macerated glands rather than being the venom itself.

We proceeded, then, on the assumption that the venom is present in the distilled water filtrate. Ether extracts from neutral, acid, and alkaline solutions yielded extremely small amounts of residue which were inert. This would appear to rule out lipoids and alkaloids. The filtrate gives positive Biuret, Millon, Adamkiewiecz, and Hopkins-Cole tests for protein, but might contain toxic non-protein constituents as well. We, therefore, next attempted to separate proteins from non-proteins by dialysis.

Collodion bags were prepared and tested to retain Congo Red. Two cc. of venom solution was placed in each bag and the bag suspended in 400 cc. of distilled water. The water was stirred frequently and changed each 24 hours, dialysis continuing for 72 hours. Control samples of venom in glass ampoules were placed in the same baths. (Control 1.) The water from the baths was evaporated to a small volume. This step was controlled by adding venom to equivalent amounts of water and evaporating for the same length of time. (Control 2.) The products were then assayed. The results are given in Table 14.

This experiment was repeated twice with the same result. The concentrated dialysates gave doubtful or negative Biuret tests, other protein tests were negative.

Since the venom is thus shown to be non-dialysable and associated with protein, our next efforts were directed toward separating the protein from any non-protein, non-dialysable substances which might be present. A great many spiders and much work were expended in these attempts, which, however, all resulted in failure, due to the extreme lability of the venom, probably indicating it to be protein which is easily denatured. Only two of the many experiments will be described, one in which the precipitating agent was sodium tungstate, the other methyl alcohol. In addition to these, precipitation with ethyl alcohol, ammo-

TABLE 13

MATERIAL	NO. OF RATS	AMOUNT INJECTED	RESULTS
Ether Extract (Yellow Oil)	2	Equiv. of 10 eggs	No effect
" " " "	2	" " 5 "	" "
Precipitate	4	" " 2½ "	50% killed
"	4	" " 5 "	100% "
Conc'd. Filtrate	2	" " 15 "	No effect
" "	2	" " 7½ "	" "

TABLE 14

MATERIAL	NO. OF RATS	AMOUNT INJECTED	RESULTS
Control Solution 1	3	Equiv. of ½ spider	All died
" " 2	3	" " ¼ "	" "
Non Dialysable Residue	8	" " ½ "	87% "
Concentrated Dialysate	4	" " 2 "	No symptoms

nium sulfate, lead acetate, and tannic acid was attempted.

Exp. 1. The venom glands of 60 spiders were macerated in 100 cc. distilled water and the solution allowed to stand over night. A small amount of white precipitate settled out which was filtered and washed. The precipitate was dissolved in saline. This is solution V-1. A portion of the filtrate was assayed as a control; this is solution V-2. To 5 cc. of the filtrate was added ½ cc. of 1% Na tungstate solution plus 3 cc. N/12 H_2SO_4. A white precipitate formed, which was filtered off, washed and then shaken up with 2 cc. 5% $CaCl_2$ to break up the protein tungstate. This was assayed as solution V-3. The filtrate from V-3 was neutralized with Na_2CO_3 and assayed as V-4. To control the effect of the addition of acid, a portion of the original filtrate (V-2) had added to it 3 cc. of N/12 H_2SO_4. It was allowed to stand the same length of time (approximately 5 minutes) as was required for the tungstic acid precipitate to form and be filtered, and was then neutralized with Na_2CO_3. This is V-5. The results are shown in Table 15.

TABLE 15

MATERIAL INJECTED	NO. OF RATS	AMOUNT INJECTED	RESULTS
V-1	4	Equiv. of 2½ spiders	2 died, 2 sick but recovered
V-1	2	" " 1½ "	Sick but recovered
V-2	2	" " 1 "	Died
V-2	2	" " ½ "	Died
V-3	5	" " 2 "	2 died, 3 recovered
V-3	4	" " 1 "	Slightly paralyzed but recovered
V-3	4	" " ½ "	No symptoms
V-4	3	" " 2 "	No effect
V-4	4	" " 1 "	" "
V-4	3	" " ½ "	" "
V-5	3	" " 2 "	" "
V-5	3	" " 1 "	" "
V-5	2	" " ½ "	" "

It will be noted that the protein precipitate, (V-3), in large doses, was toxic, but that much of the potency has been lost. The loss, we believe, can be attributed to the action of the sulfuric acid, as Solution V-5 showed no toxicity whatever. This experiment was repeated three times, there was some variation in the toxicity of the original precipitate (V-1) and of the tungstic acid precipitate (V-3), in the latter case depending upon the length of time it was left in contact with the sulfuric acid. In every case, however, addition of dilute sulfuric acid to the original venom, for a period of 5 minutes or longer, destroyed the toxicity. This point will be stressed later. Exp. 2. Szu (12) has recently reported upon the ability of methyl alcohol to precipitate proteins without causing denaturization, providing the length of time allowed for precipitation was not too great, 4 hours being permissible in some cases. An attempt to precipitate with methyl alcohol is next described.

The venom glands from 40 spiders were dissected out and macerated in 10 cc. distilled water. One cc. was assayed as a control. This is M-1. To 4 cc. of the

remainder, 100 cc. of absolute methyl alcohol was added, and the solution, with frequent shaking, left in the refrigerator for 3 hours. A white precipitate formed which was centrifuged off, washed with methyl alcohol, quickly dried, and dissolved in saline. This is M-2. Four cc. of the remainder was treated in the same way, but only left standing for 1 hour. This is M-3.

The filtrates from M-2 and M-3 were evaporated to a small volume. These are M-4 and M-5 respectively. Finally, 1 cc. of the original venom was added to distilled water and evaporated for the same length of time as the filtrates M-4 and M-5 in order to control the possible destruction by evaporation. This control is M-6. The results are given in Table 16.

TABLE 16

MATERIAL INJECTED	NO. OF RATS	AMOUNT INJECTED	RESULTS
M-1	2	Equiv. of 1 spider	Died
M-1	2	" " ½ "	"
M-2	2	" " 2 "	Paralytic symptoms, recovered
M-2	2	" " 1 "	" " "
M-3	2	" " 2 "	" " "
M-3	2	" " 1 "	" " "
M-4	2	" " 2 "	No symptoms whatever
M-4	2	" " 1 "	" " "
M-5	2	" " 2 "	" " "
M-5	2	" " 1 "	" " "
M-6	2	" " 1 "	Died
M-6	2	" " ½ "	1 died, 1 recovered

The animals receiving solutions M-2 and M-3 (that is, the protein precipitates) gave a peculiar reaction. Paralysis of the legs set in very promptly and was just as severe as in the animals given straight venom. However, they showed none of the depression which venom poisoned rats invariably show; on the contrary, they tended to remain in motion, dragging themselves around as best they could, even trying to climb the side of the cage. They showed no respiratory involvement whatever, the lachrymal glands were not affected, nor was there a discharge of bloody serum from the nostrils. Recovery from the paralysis occurred within 3 to 4 hours. So greatly did they differ from the controls and also from the picture presented by rats given sub-lethal doses of the straight venom that we are inclined to believe that there are two factors present, one of which, the more lethal, is destroyed or denatured by the alcohol, while the other, paralytic, factor is not affected. This seems the more likely as there was no difference in the behavior of groups M-2 and M-3, in spite of the fact that the former solution had been subjected to the action of the alcohol for three hours instead of only one. In other words, time did not seem to cause a progressive destruction of a simple toxic principle. This experiment was performed twice with entirely concordant results.

Experiments performed to study the action of the digestive enzymes produced further evidence of the extreme lability of the venom. As will be described later, studies of the action when venom was given orally showed it to be harmless.

We, therefore, subjected the venom to the action of pancreatin and pepsin.

The venom glands from 40 spiders were macerated in 10 cc. distilled water and one-half used for each determination. One cc. was used as control. This was C-1.

Pancreatin Digestion. A 2% solution of pancreatin and a .5% solution of sodium carbonate were prepared and the following solutions made up and incubated at 37° for six hours.

1 cc. venom plus 1 cc. pancreatin solution plus 1 cc. sodium carbonate solution = Panc. I

1 cc. venom plus 1 cc. sodium carbonate plus 1 cc. distilled water = Panc. II

1 cc. venom plus 2 cc. distilled water = C-2

1 cc. pancreatin solution plus 1 cc. sodium carbonate plus 1 cc. distilled water = C-3

The results of assay are shown in Table 17.

Peptic Digestion. A 2% pepsin and a 1/10% hydrochloric acid solution were prepared, the following mixtures made up, and incubated at 37° for six hours.

1 cc. venom plus 1 cc. pepsin solution plus 1 cc. HCl solution = Pep. I

1 cc. venom plus 1 cc. HCl plus 1 cc. distilled water = Pep. II

1 cc. venom plus 2 cc. distilled water = C-4

1 cc. pepsin solution plus 1 cc. HCl solution plus 1 cc. distilled water = C-5

The results of the assay are given in Table 18.

While both pepsin and pancreatin incubation destroy the toxicity, the important point brought out in the above experiments is that incubation for 6 hours merely in dilute acid or base also destroys the toxicity. This is in agreement with

TABLE 17

MATERIAL INJECTED	NO. OF RATS	AMOUNT INJECTED	RESULTS
C-1	2	Equiv. of 1 spider	All died
C-1	2	" " ½ "	" "
Panc. I	2	" " 1 "	No effect
Panc. I	2	" " ½ "	" "
Panc. II	2	" " 1 "	" "
Panc. II	2	" " ½ "	" "
C-2	2	" " 1 "	All died
C-2	2	" " ½ "	Both very sick but recovered
C-3	2	1 cc.	No effect
C-3	2	½ "	" "

TABLE 18

MATERIAL INJECTED	NO. OF RATS	AMOUNT INJECTED	RESULTS
Pep. I	2	Equiv. of 1 spider	No effect
Pep. I	2	" " ½ "	" "
Pep. II	2	" " 1 "	" "
Pep. II	2	" " ½ "	" "
C-4	2	" " 1 "	All died
C-4	2	" " ½ "	" "
C-5	2	1 cc.	No effect
C-5	2	½ "	" "

the point made in precipitation studies with sodium tungstate where addition of the sulfuric acid alone resulted in destruction and emphasizes the great lability of the venom and the ease with which it is denatured.

Destruction by Heat. No systematic studies were made of the degree of temperature and length of time of exposure necessary to destroy the venom. Two samples of venom were tested, one after being heated to boiling for five minutes, the other after heating to 75° for twenty minutes. In both cases the toxicity had been completely destroyed. As was noted above, heating to 37° for six hours did not destroy the toxicity.

no symptoms whatever, cannot be accepted for the reasons given earlier in the paper. We have several times permitted a spider to bite a rat without effect, the reason being that the spider was either not sufficiently irritated or had too recently exhausted her venom.

Early in June we set aside 26 rats for immunization; 10 were mature (average about 250 grams) and 16 immature, the latter representing the survivors of the toxicity curve determination. The mature animals were given $\frac{1}{4}$ spider twice weekly for three weeks and $\frac{1}{2}$ spider twice weekly for two weeks. The immatures were given $\frac{1}{8}$ spider twice weekly for three weeks and then $\frac{1}{4}$ spider twice

TABLE 19

NO. OF RATS	TYPES OF RATS	WEIGHT	AMOUNT INJECTED	RESULTS
10	Imm'd. Adults	200–250	Equiv. of 1 spider	All very sick but recovered
6	Control "	200–250	" " 1 "	" " " 1 died
16	Imm'd. Immatures	100–150	" " 1 "	" " " 6 "
4	Control "	100–150	" " 1 "	" " " 2 "

Immunology

A considerable amount of research has been done in the study of the immunological aspects of this problem, notably by South American workers. The most conclusive evidence of anti-venin production was reported by Troise (13) who injected three rabbits with 14 injections each of dry venom over a period of 37 days and found, in the most favorable case, that .05 to .1 cc. of serum would neutralize, in vitro, 1 mg. of venom. He apparently did not study the protective action of serum when injected separately, nor the question of how long a time could be permitted to elapse between the venom and serum injections.

The work of Baerg (7) in which he caused spiders to bite rats, and found that the first bite caused severe symptoms, the second bite less severe, and the third

per week for two weeks. It was thought that by this time immunization had been effected and all animals were given the equivalent of one spider each. (The immature rats at this time weighed from 130 to 150 grams.) The results are given in Table 19.

These findings indicate that little, if any immunization had occurred and that, for the rat at least, immunization is a very slow process.

The survivors of the previously injected groups were then injected for another 5 weeks period. In the mature animals the dose was $\frac{1}{4}$ spider every other day for the first 3 weeks, then $\frac{1}{2}$ spider every other day for the following 2 weeks. The immatures were given $\frac{1}{8}$ spider every other day for 3 weeks, then $\frac{1}{4}$ spider for one week and finally $\frac{1}{2}$ spider for one week, at the same intervals.

These rats were next tested for resistance by being given first, tentatively, one spider each, which they accepted without any symptoms, 3 days later 2 spiders each were given, again without effect, and finally 3 days later 4 spiders each. No symptoms whatever occurred and we concluded that either tolerance or immunity had been achieved.

In Vitro Neutralization. The resistance indicated in the preceding paragraph might be interpreted either as tolerance or as true immunity due to anti-body formation. To test which of these conditions obtained, 5 rats of each group were bled to death and the sera pooled. In other experiments we have found that the most satisfactory way to obtain the largest possible amount of blood was to cannulate the carotid, the cannula being attached to a large syringe. Gentle suction exerted by the plunger fills the syringe rapidly and clotted needles are avoided. From 8 to 10 cc. of blood is easily obtained from adult rats. This procedure was therefore employed. The blood was permitted to clot and the serum decanted. Various mixtures of serum and venom were prepared, as summarized below, and permitted to stand in the cold over night and then injected intraperitoneally into young rats (50 to 60 grams).

Preparation I. The venom from 10 spiders in 1 cc. saline plus 1 cc. immune serum.

Preparation II. The venom from 10 spiders in 1.5 cc. saline plus ½ cc. immune serum.

Preparation III. The venom from 10 spiders in 1 cc. saline plus 1 cc. serum from normal (non-immunized) rats.

Results of the injection are shown in Table 20.

TABLE 20

MATERIAL INJECTED	NO. OF RATS	AMOUNT OF VENOM	RESULTS
Prep. I	3	Equiv. of 2 spiders (8 A.L.D.)	No symptoms
Prep. II	4	" " 2 "	" "
Prep. III	2	" " 2 "	All died
Prep. III	2	" " 1 "	" "
Prep. III	2	" " ½ "	1 died; 1 recovered

The above results agree with the work of Troise, indicating that direct neutralization of the venom takes place.

Direct Injection. The remainder of the serum obtained as described above was tested by direct injection into animals injected with venom. The results are given in Table 21.

TABLE 21

MATERIAL INJECTED PER RAT		INTERVAL BETWEEN VENOM AND SERUM INJECTIONS	NO. OF RATS	RESULTS
Venom	Serum			
Equiv. of 2 spiders (8 A.L.D.)	1 cc.	10 minutes	4	No symptoms
" " 2 "	½ cc.	10 "	4	" "
" " 2 "	1 cc.	1 hour	4	Recov'd. promptly
" " 1 "	1 cc. normal serum	10 minutes	4	All died

In the third group symptoms were well

advanced by the time the serum was given. In large doses (1–2 spiders) symptoms start promptly and death may occur within 2 hours. Relief seemed to be very prompt, the animals appearing normal, except for slight residual paralysis of the limbs, within 2 hours after introduction of the serum.

The above experiment was repeated, using 8 of the remaining rats. During the two weeks interval these had been given ½ spider each every other day. The results are given in Table 22.

Attention is directed to the last group as simulating more exactly the condition encountered in the human case of arachnidism. When the venom is given subcutaneously, the symptoms are slower in making their appearance, the length of life following lethal doses is increased and the absolute lethal dose somewhat greater. At the end of three and one-half hours symptoms are, however, well advanced. The rats are comatose, bloody serum covers the nose, respiration is slow and paralysis is present. The injection of serum intra-peritoneally gives prompt relief, within 3 to 4 hours the rats are again normal. It is probable that intravenous injection of serum would give even better results, but this is difficult to perform in small rats without risking the danger either of heart puncture or anesthesia.

The results of these experiments may be summarized as follows: $\frac{1}{10}$ cc. of serum given immediately (less than 10 minutes) protects rats against the venom of 2 spider equivalents (8 A.L.D.), both being given intra-peritoneally. 1 cc. of serum will protect rats against 2 spiders if given one hour later. ½ cc. given one hour later will not protect in all cases, both being given intra-peritoneally. If the venom be given sub-cutaneously, 1 cc. of serum (given intra-peritoneally) will protect against 2 spiders even though administration be delayed for three and one-half hours. It should also be pointed out that the upper limits both for direct protection and for protection against subcutaneous injection of venom have not been reached, the figures given merely represent the lowest dosages of serum used. It is very probable that the serum is even more active than these figures indicate.

TABLE 22

MATERIAL INJECTED		INTERVAL BETWEEN VENOM AND SERUM INJECTION	NO. OF RATS	RESULTS
Venom (Spider Equiv.)	Serum			
2 (8 A.L.D.)	¼ cc.	10 minutes	4	No symptoms
2 "	$\frac{1}{10}$ cc.	10 "	4	Slight paralysis, not really sick, prompt recovery
2 "	½ cc.	1 hour	4	3 recovered; 1 died
2 Inj'd. Sub-cut.	No serum		4	All died
2 Inj'd. Sub-cut.	1 cc. Intraperitoneally	3½ hours	4	All recovered

Placental Transmission of Anti-bodies. Two rats of the immunization series became pregnant and had their litters about the time that the last group was sacrificed (about 12 weeks immunization). The litters were saved until they reached a weight of 50–60 grams and were then injected, along with controls, as indicated in Table 23.

This would apparently indicate some degree of transmission of antibodies, either through the placenta or in the

milk, although the immunity is not of very high grade.

Immunization with Eggs and Cross-immunization. Parallel with the venom-immunized rats, another group was injected with sub-lethal amounts of eggs. Injections were commenced with $\frac{1}{4}$ egg each week for five weeks. Immunization appeared rather more promptly than in the venom-immunized group; tests with lethal doses at the end of five weeks caused slight symptoms only. Injection of two eggs per dose was given twice weekly for an additional five weeks, when the animals were tested for immunity. A maximum of 16 eggs per rat gave slight symptoms only with prompt recovery. Control rats of the same weight were killed by 8 eggs.

The serum from sacrificed rats was next tested for its neutralizing power in vitro. The following mixtures were prepared and permitted to stand over night.

Prep. I: 50 eggs macerated in 5 cc. saline, mixed with 5 cc. serum from egg-immunized rats.

Prep. II: 50 eggs macerated in 5 cc. saline mixed with 5 cc. serum from venom-immunized rats.

Prep. III: 50 eggs macerated in 5 cc. saline mixed with 5 cc. normal serum.

Prep. IV: Glands from 10 spiders macerated in 1 cc. saline plus 4 cc. serum from egg-immunized rats.

Results of the assay are given in Table 24.

The results show a neutralizing action of homologous serum upon the egg poison, and also that the two poisons are distinct; neutralization of egg poison by venom-immunized serum does not occur, nor does the reverse.

Direct injection of egg-immunized serum is also protective, as is shown in Table 25; the limit of protection was not tested for.

Commercial Anti-serum. From the results described in the previous section, the commercial preparation of an anti-serum against the venom of the black widow appeared to be feasible. Even though the fatality rate in arachnidism of this type is low, the fact remains that it is occasionally fatal. Our work indicates

TABLE 23

RATS USED	NO. OF RATS	AMOUNT OF VENOM	RESULTS
From Immunized Mothers	3	1 spider	2 died; 1 sick but recovered
" " "	3	$\frac{1}{2}$ "	Sick but recovered
Controls	3	1 "	All died
"	3	$\frac{1}{2}$ "	" "

TABLE 24

MATERIAL INJECTED	AMOUNT OF POISON	NO. OF RATS	RESULTS
Prep. I	Equiv. of 5 eggs	4	No symptoms
Prep. II	" " 5 "	4	All died
Prep. III	" " 5 "	3	" "
Prep. III	" " $2\frac{1}{2}$ "	3	" "
Prep. IV	" " 2 spiders	2	" "
Prep. IV	" " 1 "	2	" "

that a bite would be more likely to be fatal in children and young children are particularly likely to be bitten, being ignorant of the danger and curious as to the spider. Aside from the prevention of a fatal outcome, the promptness with which symptoms disappear in the rat following the administration of serum assay, made after about ten weeks injection, are given in Table 25a.

These results indicate that already a serum of considerable potency has been produced, although, of course, its efficacy in the human remains to be demonstrated by clinical trial. This work is being continued.

TABLE 25

MATERIAL INJECTED		NO. OF RATS	RESULTS
Eggs	Serum		
2	None	4	All killed
5	1 cc. within 10 minutes	3	No symptoms
10	1 " " 10 "	3	No "

TABLE 25a

NO. OF RATS	VENOM		SERUM		RESULTS
	Amount	Mode of Injection	Amount	Mode of Injection	
4	¼ spider	Intra-per.	None		3 killed
4	½ "	"	"		All "
2	2 "	"	½ cc. #2	Intra-per. in 5 min.	Recovered
2	2 "	"	½ cc. #3	" " " "	"
4	2 "	"	¼ cc. #2	" " " "	"
4	2 "	"	¼ cc. #3	" " " "	"
4	2 "	"	1/10 cc. #2	" " " "	All died
4	2 "	"	1/10 cc. #3	" " " "	Recovered
2	2 "	Sub-cut.	None		Died
2	2 "	"	½ cc. #2	" " " "	"
2	2 "	"	½ cc. #3	" " " "	1 died
2	2 "	"	1 cc. #2	" 3½ hours	Recovered
2	2 "	"	1 cc. #3	" " "	"

would further recommend it as a therapeutic agent.

We were fortunate in interesting the E. R. Squibb and Sons Company in the problem and a cooperative project was undertaken, in which we collected the spiders and sent them the dried venom glands. They began the injection of two sheep in the late summer, starting with small doses of venom and gradually increasing the dose. The results of the first

Toxicology

Symptomatology. The effect of the black widow spider venom upon the organism has been variously described by different investigators. In the human Bogen (2) has studied a considerable series of cases and finds that the chain of symptoms is a remarkably constant one. The outstanding features in the sequence of events are as follows: The bite itself is not painful,

being comparable to a sharp pin prick; a dull numbing pain ascends the extremity bitten, and then localizes itself in the muscles of the chest, back and abdomen. This pain is excruciating in character. The abdominal wall is board-like in its rigidity; except for the absence of local tenderness and the involvement of other muscle groups the pain resembles that experienced in the case of a ruptured appendix or perforated peptic ulcer. Due to the spasm of the thoracic muscles respiration is difficult. A rise in blood pressure occurs, there is frequently nausea and vomiting, a slight fever and leucocytosis. The general symptoms make their appearance within four hours and may last for two to three days. In fatal cases death occurs in from 18 to 36 hours. The observations are in general agreement with those of Baerg (7) and of Blair (1) who permitted spiders to bite them under controlled conditions. Relief from pain seems to be difficult to obtain, relatively large doses of morphine are without much effect; hot baths are very helpful.

In the rat, administration of the venom is followed by paralytic symptoms which are first evidenced by a peculiar stiffness of gait and awkwardness in movement. The hind legs are first affected and the animal walks with the rear elevated. One or both forelegs are next affected and the animal sits in a hunched up position with the forelegs bent and held close to the body. At this time the animal refuses to move unless violently stimulated but can withdraw the foot if the toes be pinched. As regards respiration, we noted a difference in behavior usually depending upon the size of the animal. In immature rats the respiration becomes progressively more and more shallow, the animal lies in a state of coma; as death approaches, the breathing becomes almost imperceptible. In older rats respiration becomes extremely labored. The animal gasps violently for air but is apparently unable to fill the lungs. This labored respiration continues until death occurs. Many rats were autopsied immediately after death. In all cases the lungs collapsed when the thorax was opened, indicating no constriction of the bronchioles, although, as will be noted later, ephedrine appeared to give considerable relief. The auricles were usually beating. There were no gross signs of pathologic changes.

One effect which was invariably produced was an irritation of the lachrymal glands. The eyes watered profusely; they were usually closed or nearly so. There was always an accumulation of bloody serum around the nostrils, frequently in considerable amounts. This happened even when there was no labored respiration. The animals suffered from thirst and in the earlier stages made efforts to drink but were apparently unable to swallow.

Antidotes. No extensive study of antidotes was possible in the time available; however, a few drugs which for one reason or another suggested themselves, were tested. So far as we are aware no specific antidote is known. Mature rats (200–250 grams) were used in the following experiments. Table 26 summarizes the results.

Sodium amytal and scopolamine were used because of their depressant action upon the central nervous system. Dinitrophenol was tried in the hope that the high basal metabolism which it induces might lead to a more rapid destruction of the venom. Methylene blue was tried because one experiment in which the venom was hydrolyzed and tested with Fehling's solution gave a positive test. (This result could not be confirmed later, but at the time suggested the possibility that a

glucoside bearing a cyanide group might be responsible.) Congo Red was employed because of its known action of absorbing bacterial toxins. Curare, because it seemed possible that its paralytic effect on skeletal motor plates might be antagonistic to the possible irritating effect of the toxin.

The only agent which seemed to be of value was ephedrine; however, only three animals were used and it was unfortunately too late to conduct an extensive experiment. Its action was apparently to give relief from the extreme dyspnea. This experiment should be repeated and extended.

Oral Administration without Effect. Food and water was withheld from 8 rats, the former for 48 and the latter for 24 hours. Four rats were then given small amounts of water containing venom and corn meal moistened with a venom solution, which they consumed readily. The total amount consumed within thirty minutes was the equivalent of 8 spiders each. No effects whatever were observed. The other four rats were given macerated eggs, they refused to drink the water solution, but ate the food containing eggs in amounts up to 20 eggs each, also without effect. In view of the results reported under chemistry, the destruction of the venom probably takes place in the stomach, being effected by the acid present. The egg globulin is presumably destroyed in digestion.

Effects upon Blood. Red and white counts and coagulation time determinations (capillary) were made every other day for one week on four rats. Two were then injected daily for four days with sub-lethal doses of venom and the other two with sub-lethal amounts of eggs. The amount given varied with the condition of the animals, but was sufficient to keep them in an almost moribund condition. Red and white counts and coagulation time determinations were made in duplicate daily during the injection period. The results are shown in Table 27.

The red count was not affected. The white count, as might be expected, fluctuated widely; generally speaking, however, there was a slight leucocytosis during

TABLE 26

NO. OF RATS	ANTIDOTE TESTED	AMT. VENOM	RESULTS
12	No Antidote (Controls)	Equiv. of 2 spiders	All died
5	Sodium Amytal 12.5 mg.	" " 2 "	4 died; 1 recovered
4	" " 6 mg.	" " 2 "	All died
3	Scopolamine hydrobromide 1/50 grain	" " 2 "	All died, the treated animals lived 2 days longer
2	Dinitro phenol 4 mg.	" " 2 "	Died sooner than the controls
3	Methylene blue .2–.4 cc. 1% solution	" " 2 "	All died
2	Congo Red .2–.4 cc. 1% solution	" " 2 "	" "
3	Curare .2 mg.	" " 2 "	" "
1	Ephedrine sulfate 6 mg. in 2 doses ½ hour apart	" " 2 "	Recovered
2	Ephedrine sulfate 3 mg. (1 dose)	" " 2 "	1 died; 1 recovered
2 (wt. 50 grams)	Calcium gluconate 20 mg. immediately plus 20 mg. ½ hour after venom injection	½ spider each	Both died

the first day or two of the injection period, which later subsided. The coagulation time was increased somewhat, probably not significantly.

Body Temperature. The rectal temperatures of 2 rats were taken at 15 to 30 minute intervals following the injection of lethal doses of venom. A progressive fall of about one-half degree per hour resulted, reaching just before death a level of 94.6 in one and 93.6 in the other rat.

Muscle Nerve Preparation. Several experiments were performed in which the effect of venom upon muscle-nerve preparations of the frog was studied. The results were negative and may be briefly summarized. 1. Injection of venom directly into the muscle caused no contraction. 2. After testing for the minimum effective electrical stimulus, soaking the nerve in a venom solution (in saline) neither increased nor decreased its irritability. 3. An entire muscle-nerve preparation soaked for 30 minutes in a saline solution of venom behaved the same as a control preparation kept for an equal length of time in saline. These findings, which are by no means conclusive, support the view that the action of the venom upon the musculature is by way of the central nervous system rather than peripherally.

TABLE 27

POISON INJECTED	RED COUNT IN MILLIONS				WHITE COUNT IN THOUSANDS				COAGULATION TIME (MIN.)			
	Control Period		Injection Period		Control Period		Injection Period		Control Period		Injection Period	
	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High
Rat #26 Eggs	9.6	11.3	9.2	9.4	8.1	8.7	6.6	10.6	1.40	1.50	1.45	2.45
Rat #6 Eggs	8.4	10.0	8.9	9.3	6.0	12.0	7.5	13.0	1.50	2.00	1.50	2.5
Rat #76 Venom	7.4	10.0	8.3	9.6	8.1	10.6	8.0	13.7	1.40	1.50	2.05	2.5
Rat #11 Venom	8.6	9.6	8.5	9.0	6.0	8.7	9.0	15.0	1.35	1.50	2.00	3.20

TABLE 28

FRESH EGGS		DRIED PRECIPITATE	
Concentration	Time	Concentration	Time
1:100	20 seconds	1:2000	1 minute, 10 seconds
1:200	20 "	1:4000	2 " 15 "
1:500	35 "	1:6000	5 " 30 "
1:1000	55 "	1:8000	8 " 40 "
1:2000	1 minute, 55 "		
1:4000	5 "		
1:10000	25 "		

Hemolytic Action of Egg Poison. Studies of the rate of hemolysis of the protein from fresh eggs, and of the dried, precipitated protein were made, also of the anti-hemolytic action of the serum from egg-immunized rats. A suspension of rat red cells was used in these experiments. The results are given in Table 28.

The 1:6000 concentration of dried egg precipitate was used as the test solution

for the study of the anti-hemolytic action of egg-immunized serum. The results are given in Table 29.

Since at this dilution the hemolysin is effective within 5 minutes and 30 seconds, it can be stated that the anti-hemolysin is capable of neutralizing it at a concentration of 1:10,000.

TABLE 29

CONCENTRATION OF SERUM	TIME
1:20	Had not occurred at end of 2 hours
1:100	" " " " " " 2 "
1:500	" " " " " " 2 "
1:1000	40 minutes
1:5000	30 "
1:10000	8 "

Pathology

Several rats were kept chronically intoxicated with venom for four days. They were then killed by administration of a lethal dose, the following structures removed and sectioned: heart, lungs, liver, spleen, stomach, small and large intestines, kidneys, adrenals, gonads, brain, and spinal cord. Histological study of these sections revealed very little; small areas of necrosis in the liver and a few swollen and hyper-chromatic cells in the motor region of the brain and anterior horns of the chord being the only pathologic findings. A rat was then kept intoxicated for two weeks, being given approximately 8 spiders during this period. The original weight was 188 grams, the final weight 121 grams. Autopsy revealed no gross pathologic lesions. The same structures as listed above (ovary and uterus) were removed and sectioned. Again very small necrotic areas in the liver were found. Special staining methods were employed for the central nervous system, but no pathologic abnormalities could be discovered. No significance is attached to the liver injuries as they were slight and might have been due to other causes.

These studies were carried out at the University of Colorado School of Medicine, under the direction of Doctor James J. Waring, to whom our great appreciation is herewith expressed.

DISCUSSION

The questions we have been asked most frequently as the fact of our investigation of the spider became known were these: 1. Are the spiders increasing greatly in numbers? 2. Is the spider changing its habits, that is, is it leaving its rural haunts and invading settled communities to a greater degree than before? 3. What methods of eradication are feasible? 4. Does the spider represent a real menace? 5. Is there any effective antidote? 6. What are the possibilities of anti-venin? To the first question the authors do not hesitate to give an affirmative answer. This may appear unjustified since this is admittedly the first year in which we have collected the spider. If the black widow were smaller, if its appearance were not so striking, if it were easily confused with some other form, or if it had previously been fairly common, one might hesitate to commit himself. However, as an example, we have a cold box set just outside the laboratory, on the ground level, and opening into the room by means of a window. So far, we have on two different occasions found three spiders at one time and another time two spiders, in webs close to the window. They are visible all the way across the room. When opening the window, one must be blind not to see them. This box has been there for years. We feel morally certain that had spiders ever been in the

same location before we would have noticed them.

It is of course true that one sees what one looks for, and the newspaper publicity which these spiders have received has caused many more of them to be noticed and reported than would otherwise have been the case. On the other hand, farmers and fruit growers are usually quite observant as to the kind of insects found on their crops and when this year, for the first time, reports are received that tomato growers find the spiders so bad that protective clothing must be worn, when grape growers report that in some places the spiders are so numerous that the pickers refuse to work, and the grapes are rotting upon the vines, and peach growers notice many of them in their orchards, the conclusion seems inescapable that they are more numerous this year than ever before.

The second question, relating to an apparent change in the habits of the spider, in that it seems to be invading settled communities to a greater degree, is to some extent dependent upon the first. If the spiders in a given region increase greatly in numbers, their manner of dispersal by wind and their utilization of such means of transportation as box cars would make it inevitable that some would find themselves within towns and cities. Once having become established, their chances for survival and increase are favored. Many of them have been found in basements, garages and similar places where they are protected against the cold to a much greater degree than would be the case out in the open. We believe that the increase in numbers noted during the past summer is due to the mild winter which preceded it; however, cold will not operate as a check upon those which have established themselves in the garages and basements of heated buildings. The conclusion appears inescapable that, unless drastic methods of eradication are employed, we will have a considerable, and probably an increasing number of these unwelcome guests.

This leads to the problem of eradication. We have tested, under laboratory conditions, several of the more common insecticides. The general conclusion was that such insecticides as Flit and Black Flag, in concentrations sufficient to kill promptly all flies within the room, is without effect upon spiders, as would be expected from the difference in the anatomy of the respiratory organs. Sulfur dioxide, in high concentration, will kill them in time, as will carbon disulfide, though relatively high concentrations and long exposures are necessary. Often the spider appears to be dead and remains so for hours but eventually recovers. Hydrogen cyanide, in the form of cyanogas, is effective, but too dangerous to recommend for general use. The California State Department of Health recommends the use of creosote and crude oil sprays, which would no doubt be effective in certain locations, but are obviously unavailable in vineyards or tomato beds. The spider is far from gregarious in its habits and consequently a given basement or garage will not harbor more than perhaps a half dozen. Our suggestion, when called upon for advice, has been to locate the individual spider, easiest done at night, and destroy it, rather than resort to general fumigation. This advice is valueless for the aforementioned farmer or fruit grower; protective clothing during the picking season and burning of debris afterward is about all that can be suggested.

Does the spider represent a real menace? We have emphasized throughout, in our dealings with the press and public, the fact that the spider is above all extremely timid. We have rarely seen a spider,

disturbed in her web, who made any pretense of defense, to say nothing of attacking. They will almost invariably run and hide and remain out of sight in a crevice or hole for hours afterward. The danger lies in accidentally squeezing one when picking up some object to which the spider is clinging, when putting on old clothing left hanging in a shed, or in some similar way. Some children enjoy catching and playing with crawling things, which cannot be done with impunity with the black widow. As to the bite itself, there can be no question of its frequently serious, sometimes fatal, effects. The statement sometimes heard, even from zoologists who should know better, that the bite of a black widow is no more dangerous than that of a mosquito, must, in view of extensive clinical experience, be branded as false and dangerous.

There is, at present, no effective antidote. First aid treatment might well comprise the application of a tourniquet, free incision and the sucking out of the venom either by means of the mouth or some mechanical device. However, as Bogen has emphasized, the spider usually lives in filthy surroundings and the danger of infection is consequently great. Thorough sterilization of the site of the wound should therefore precede incision. Further treatment is best carried out in a hospital; it consists mainly of measures taken to alleviate pain, the free use of morphine, hot baths, etc.

The possibilities of anti-venin. Bogen gives data on the use of convalescent serum in a series of cases in California, from which he concludes that its use has to some extent aided the patient; however, it is doubtful whether the number of cases is adequate to prove the point statistically. At least as far as the rat is concerned immunity develops very slowly; it will be recalled that five weeks injection of sub-lethal doses granted little, if any, protection and that it was necessary to continue the injections for nearly three months before a really high grade immunity was developed. It is, of course, quite possible that immunity develops more rapidly in the human, but it seems doubtful that convalescent serum would ever contain as high a concentration of anti-bodies as could be produced artificially. The question of ready availability of convalescent serum must also be considered. In California, with its relatively high incidence of arachnidism, this might not present a problem, but in other regions the situation would be more difficult.

In this connection, a letter received from the mother of a spider victim is of interest. She states that her son was bitten upon the leg two summers ago. He became seriously ill, showing the typical symptoms, but recovered. Last summer he was again bitten, this time on the hand, he again was very ill but recovered. The interesting point is that the site of the first bite became badly swollen and painful at the time of the second bite, apparently indicating a local sensitization to the venom.

The serum at present being developed by the E. R. Squibb and Sons Company must await clinical use before its efficacy in the treatment of arachnidism will be known. The potency already obtained compares well, on the basis of lethal doses neutralized, with certain commercial snake antivenins. It appears likely that the principles involved in the use of snake antivenin, particularly the time factor, will apply to spider antivenin. If, as Blair believes, the absorption of the venom is by way of the lymphatics, it seems probable that superficial injection of the antiserum immediately, in the immediate vicinity of the bite, offers the best hope of success.

SUMMARY

An investigation of the natural history of the black widow spider and certain properties of its venom are described. The salient points resulting from this study are:

1. The appearance of the spider is illustrated by plates and certain of its breeding, nesting, and distribution habits described.

2. The toxicity of the venom was accurately determined.

3. Chemical studies indicate the toxic principle to be a protein, probably an albumen.

4. Various antidotes were tested, the tests resulting negatively.

5. The preparation of a potent antivenin from the rat is described and a preliminary report covering similar results in the sheep is presented.

6. The venom is shown to be chemically and serologically distinct from the poisonous principle of the eggs.

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THE PROBLEM OF CYCLOPIA

PART I

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I. INTRODUCTION

THE history of teratology, which is concerned primarily with the study of abnormal or monstrous forms of development, parallels in a general way the history of embryology itself, since it is essentially but a subdivision of the latter. It, too, was blighted by the doctrine of preformation, but it suffered, in addition, a series of handicaps from which it has only recently been freed. In spite of the fact that Aristotle, with characteristic acumen, had insisted that 'monstrous' forms must arise in conformity with natural laws manifested in an unusual way, the notion tenaciously persisted that developmental abnormalities were the result, if not of supernatural, at least of phenomena which were not to be accounted for by the operation of the ordinary and accepted 'laws' of development.

The subject was in a truly chaotic state in the early part of the nineteenth century when, through the studies of Etienne and Isidore Geoffrey St. Hilaire (1826, 1832–37), some order was brought into the confusion which existed as to the interpretation of anomalous development. They first made clear that abnormalities may be classified into fairly well-defined types. While there is no sharply defined delimitation of types each exhibits a rather uniform plan of organization. They also showed (1826, 1832–37) that the course of development might be experimentally modified with the resultant production of abnormal forms similar to those spontaneously occurring and hitherto sometimes ascribed to an abnormal preformation of the germ.

Some years later this achievement was followed by an equally great one of a countryman of theirs, Dareste, who in a truly remarkable work published in 1877, described the successful experimental production of monsters on a large scale, but more important than this, pointed out clearly the logical approach to their study.

> The anomaly and the monstrosity appear at certain epochs of development as a result of a modification in the evolution of an isolated organ or of a more or less considerable number of organs. They are the result of a change in the direction of the force which determines the successive appearance and the coördination of different parts of the embryo. The teratogenesis, or in other words, the embryogenesis of anomalous beings, must then consist, like that of normal beings, of direct study of the successive changes which development determines in the organism.

Time has only served to emphasize the essential soundness of Dareste's position.

Much of the indifference with which the modern embryologist tends to regard the study of abnormal development is due to the fact that in the past premature efforts have been made to ascertain a specific 'cause' for an anomaly, disregarding the fact that an anomaly usually represents a response of the developing organism to unusual or abnormal conditions, and that a variety of environmental factors by evok-

ing a relatively slight deviation from the normal in relatively early stages of development, may entail a series of increasingly serious developmental aberrations in later stages due to the suppression of, or interference with, normal developmental interactions and correlations, some of which have recently been so beautifully demonstrated by experimental workers in embryology. When the conditions under which specific anomalies are produced have been determined, the developmental aberrations described when they first appear, and their influences upon the later progress of developmental correlation and integration ascertained in the light of what is known to occur during normal development, progress has at least been made in their elucidation. The determination of a 'first' or 'primary cause' may well await a more complete knowledge.

While progress in the study of anomalous development must, for the most part, follow after advances in the knowledge of normal development, the operation of the factors influencing normal development may often be made more vivid by a demonstration of the consequences of their abnormal manifestations. In illustration one might cite the work of Holtfreter ('33d) who has demonstrated by the study of amphibian exogastrulae the profound effect of the roof of the archenteron upon the differentiation of the neural plate, a fact which had been previously made clear by Spemann's ('24, '31) researches, but which is now made possibly more convincing. Holtfreter's ('33c) work now makes possible a great advance in the interpretation of certain forms of anomalies the genesis of which has hitherto not been clearly understood.

Another equally interesting illustration is afforded by Cyclopia, an anomaly which for a long time has engaged the attention of embryologists, and to an analysis of which the present review will be devoted.

The Morphology of Cyclopia

Cyclopia is an anomaly, the salient characteristic of which is the presence of a single median eye situated in the middle of the face in the position normally occupied by the nose. It is to be distinguished from *monophthalmia asymmetrica* characterized by the presence of a single, laterally placed eye, its counterpart having failed to develop.

FIG. 1. CYCLOPEAN WOMAN FROM REISCH'S MARGARITA PHILOSOPHICA, BASEL, 1508

Cyclopia has, doubtless, occurred among all the vertebrates, including man, since first they were evolved, and the deep impression it made upon the minds of the ancients is attested by the fact that the term itself is derived from Homer's mythical race of one-eyed giants, the Cyclops, who, we are probably safe in assuming, have some basis in fact. Hesiod, too, mentions the Cyclops, as does Pliny, and since then literature is rich in allusions to that picturesque, though imaginary race.

Aristotle, strangely enough, does not describe cyclopia but descriptions of cyclopean monsters are not uncommon in the writings of the natural philosophers of the sixteenth and seventeenth centuries. They are, however, typically inaccurate

and often fanciful. For example, in the figure of a cyclopean woman, published by Gregor Reisch in his MARGARITA PHILOSOPHICA in 1508, (fig. 1), the eye is placed *above* the nose, a condition never actually realized as will be pointed out later. The figure further passes the bounds of credence in that the cyclops is represented as a mature woman, while the figures grouped about her bear further witness to the gullibility characteristic of writers of the period. Another, more nearly accurate figure with respect to the relation of nose and eye, taken from the second edition of Licetus' (1577–1657) DE MONSTRORUM CAUSSIS (1634), is reproduced in figure 2. The description of two eyes in the dorsal side of the head of this specimen is doubtless based on a misconception.

FIG. 2. THREE VIEWS OF A CYCLOPEAN INFANT FIGURED BY LICETUS IN HIS DE MONSTRORUM CAUSSIS, ETC., 1634

In contrast to Reisch (fig. 1) the nose is correctly placed above the incompletely cyclopean eye. A fanciful feature is the depiction of two eyes on the dorsal side of the head, as shown in the view on the left.

Relatively few descriptions of cyclopia were published during the eighteenth century (Ballantyne, '04). They are, for the most part, contained in rare publications, not represented even in fairly large collections and, therefore, rather inaccessible. Judging from references in Meckel (1826) and Huscke (1832), however, many of the eighteenth century publications present rather complete and creditable anatomical descriptions of the anomaly. A voluminous literature has, however, appeared since the beginning of the nineteenth century. No attempt will be made to exhaustively review it since it consists in large part of purely gross anatomical descriptions of the anomaly in various animals, accompanied by oftentimes unsound speculation as to its causes. Due to the interest the subject has aroused we are now provided with fairly adequate descriptions of the anomaly in almost every vertebrate class (reptiles excepted?), references to which are to be found in the works of Ballantyne ('04), Schwalbe ('13), Seefelder ('27), and Wright and Wagner ('34). A survey of the literature reveals the important fact that just as in all vertebrates a fundamentally similar plan of organization exists, so too, cyclopia exhibits an essentially similar pattern or, in other words, a characteristic deviation from the normal pattern, in all vertebrates (figs. 3 to 5, 12e). In this lies the peculiar importance of the anomaly from an analytical viewpoint. It permits, too, a generalized description which in its essential features holds true for all forms.

In so called *cyclopia perfecta* the eye is perfectly single in all its parts (Ballantyne, '04, p. 395), possessing a single cornea, pupil and lens, and revealing in other respects also no evidence of doubling (figs. 3, 4, 8, 10). The single median eye, however, is but one component of a complex of abnormalities affecting the entire prechordal region of the head (Cotronei, '22a, b; Adelmann, '34), all of which must be considered for an adequate conception of the nature of the anomaly. The external nose is often lacking, or when present is situated *above* the eye. (Allan's ('48) case is probably no exception). The

nasal chamber, too, is single, often failing to communicate with the pharynx. The brain exhibits such constant and typical malformations that Schwalbe and Josephy ('13) regard them as constituting the most characteristic feature of the anomaly. The forebrain, in perfect cyclopia, is never divided into hemispheres but consists of a simple sac enclosing an undivided ventricle; the diencephalon also being markedly abnormal in form to varying degrees. The midbrain, however, may approximate the normal. The more caudal subdivisions of the central nervous system, disregarding certain deviations in the pattern of the tracts, are rarely affected, except in cases where the embryo as a whole exhibits evidences of severer and more or less generalized abnormalities (Stockard, '10a). Stockard ('09b), however, believes that in *Fundulus* cyclopia may be accompanied by a perfectly normal forebrain. If this is so the fishes constitute an exception to a rule which seems to hold invariably in other forms, and even for some fishes according to Gemmill ('06) and Werber ('16b).

It is still doubtful whether the hypophysis is present in cyclopia perfecta. It is usually absent (Phisalix, '89) and where its presence is reported the eye shows some evidence of doubling. The epiphysis may be present or absent.

The optic nerve is variable in behavior, being sometimes present as a single strand, or often entirely absent. In younger stages the eye is often attached to the brain by the tapetum (pigment layer of the retina) with no indication of the presence of an optic stalk (Spemann, '04; Stockard, '09b; Fischel, '11, *et al.*).

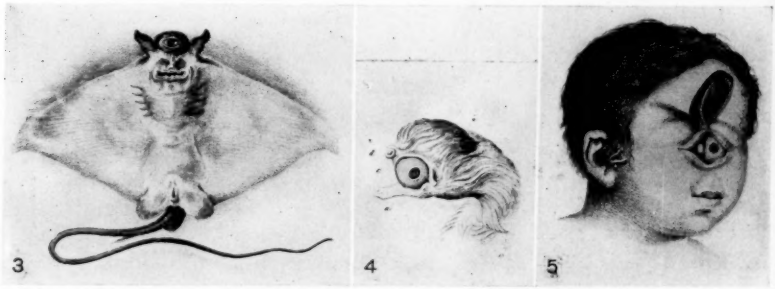


FIG. 3. CYCLOPEAN RAY, MEASURING 20 CM. TO THE BASE OF THE CAUDAL FIN, DESCRIBED BY PAOLUCCI, '74

FIG. 4. CYCLOPEAN DUCK FROM BLUMENBACH'S COLLECTION, ILLUSTRATED BY HUSCHKE, 1832. The protuberance above the eye is the nose.

FIG. 5. CYCLOPEAN HUMAN FOETUS WITH WELL-FORMED JAWS AND MAXILLARY REGION (VROLIK, '49) There was but a single optic nerve.

The olfactory nerve, or rhinencephalon, also may be present as a single rudimentary tract or entirely absent.

The third to the twelfth cranial nerves are usually present. The third and fourth are occasionally absent (Chidester, '14) and when present sometimes anastomose medially (Phisalix, '89; Mall, '17), a condition possibly correlated with fusion of the eye muscles. The latter are apparently variable in development, an interesting feature being the tendency of those innervated by the oculomotor nerves to fuse (Wilder, '08; Mall, '17).

It is perhaps unnecessary to remark that the skeletal elements of the head are also abnormal, but since these abnormalities are, in all likelihood, secondary to antecedent malformation of the eye, olfactory organ and brain, they need not be dwelt upon. Detailed accounts will be found in Schwalbe ('13), Ballantyne ('04), and Wright and Wagner ('34).

The marked tendency for cyclopia to be accompanied by malformations of the mouth, lower jaws and, in severer forms, of the maxillary region in the condition commonly known as otocephaly (fig. 6) is,

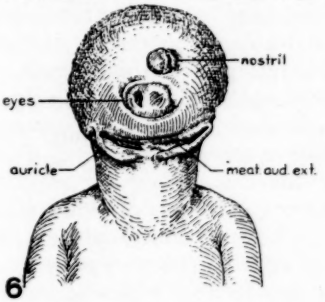


FIG. 6. OTOCEPHALIC HUMAN FOETUS (STREETER, '22)
In addition to a high degree of synophthalmia there is a complete arrest in the development of the greater part of the mandibular arch, with the result that the auricles maintain their original embryonic position.

as will subsequently be pointed out, probably a feature of fundamental significance. The abnormalities of the mouth and lower jaws of Stockard's ('09b) cyclopean *Fundulus* embryos are evident in figure 8. Otocephaly, as defined by Josephy ('13) is a condition characterized by the rudimentary development or complete lack of the lower jaw. The mouth is consequently often imperfectly developed and the ears show a tendency to approximate or fuse. While otocephaly need not necessarily accompany cyclopia, the coincidence is so marked that it is difficult to escape the suspicion that the two anomalies are closely related. For an excellent account of various degrees of otocephaly in the guinea pig and their relation to cyclopia the reader must be referred to a recent paper by Wright and Wagner ('34).

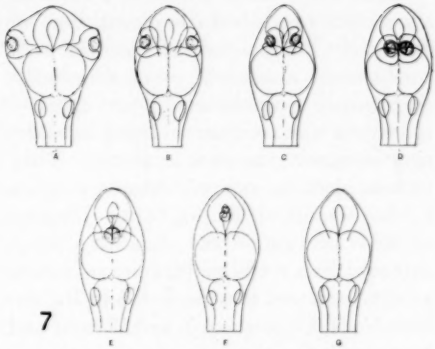


FIG. 7. DIAGRAMS (FROM STOCKARD, '09) OF THE VARIOUS DEGREES OF THE CYCLOPEAN DEFECT SHOWN BY "MAGNESIUM EMBRYOS" FROM THE NORMAL A TO COMPLETE ABSENCE OF THE EYES G.

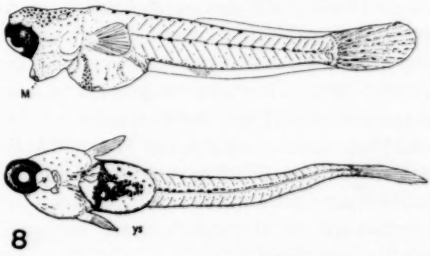


FIG. 8. LATERAL AND VENTRAL VIEWS OF A FREE-SWIMMING FUNDULUS (FROM STOCKARD, '09)
The mouth *M* is deformed, the eye perfectly single, possessing one lens and one pupil.

Between the perfect cyclopean and the normal condition a complete series of intermediate conditions may be recognized (fig. 7). Increasing degrees of doubleness of the eyes tend to be accompanied by increasingly normal conditions on the part of the other organs of the prechordal region of the head. Kundrat ('82), Fischel ('21), Adelmann ('34) and

others have pointed out the fact that the degree of malformation of the brain tends to parallel closely the degree of approximation of the eyes. However, cerebral anomalies are not always accompanied by cyclopia (Wright and Wagner, '34).

Aside from the complex of anomalies above described, which constitute an essentially integral part of the cyclopean condition, a number of other abnormalities, which are obviously not causally related to it, have been reported as occurring in connection with cyclopia. They include among others, hare-lip, spina bifida, umbilical hernia, situs inversus of the viscera and uterus unicornis. More extended lists with appropriate references to the literature may be found in Ballantyne ('04), Ognew ('30), and Wright and Wagner ('34).

The single median eye of cyclopia perfecta may vary considerably in size, being often somewhat larger than a normal eye, often smaller but normally formed, and sometimes rudimentary and abortive, being sometimes represented by only a tapetal sac. This latter condition is but a step removed from one characterized by complete absence of the eye (Anophthalmia mediana). With asymmetrical forms, exhibiting unilateral microphthalmia or suppression of the eye, we are not primarily concerned.

A number of authors have endeavored to establish satisfactory classifications of cyclopean and related monsters (Vrolik, '49; Geoffroy St. Hilaire, '32–'37; Bock, '89; Blanc, '95). These are conveniently summarized by Schwalbe and Josephy ('13), but due to the fact that cyclopia and various associated anomalies often intergrade, none has been universally adopted. We follow Mangold ('31) in adopting the simple classification of Werber ('15), distinguishing six degrees, (1) Synophthalmia bilentica, (2) synophthalmia unilentica, (3) cyclopia synophthalmia, (4) cyclopia perfecta (monophthalmia mediana), (5) microphthalmia mediana, (6) Anophthalmia mediana (see fig. 7).

Relative Frequency of Cyclopia

Little can be said concerning the relative frequency of cyclopia in the various vertebrate species. It has been observed and described more frequently in man and the pig (Schwalbe and Josephy, '13, p. 210) than in other forms, which is perhaps only natural; but obviously a survey of the cases described in the literature can yield no reliable figures as to the absolute or relative incidence of the anomaly. The figures would merely indicate in a general way the relative frequency of opportunity to observe the anomaly. Such is obviously the case in the compilation of Hannover ('82) where of 268 cases, there were 103 human foetuses, 130 pig, 51 lamb, 22 dog, 12 cat, 10 horse, 9 goat, 3 rabbit, and 1 deer foetus. Somewhat more significant figures, derived from Panum ('60), are given by Mall ('08) for man; in a group of 618 human monsters, 16 were cyclopic and 9 anophthalmic. In Mall's own cases, three of forty-eight embryos had "misplaced eyes". The figures of Wright and Eaton ('23) reveal a .2 per cent incidence of otocephalic monsters (cyclopean included) among about 40,000 guineapigs; in one branch of this strain the percentage ran about 27 per cent. However the figure for cyclopia would be only a fraction of the above figures.

Viability of Cyclopean Monsters

Human cyclopean monsters, as a general rule, survive, if at all, for only a few hours after birth. Von Hippel ('00) records one, however, which is said to have lived ten years! The severity of the anomaly in this case is not stated. Whether the

abnormality of the brain, in higher forms at least, is responsible for their speedy demise, is uncertain. In fishes, amphibia and other yolk-rich forms, they are able to survive in almost every instance only as long as a supply of yolk remains, for the mouth is almost invariably imperfect. Stockard states that many *Fundulus* embryos showing a cyclopean defect hatched normally, were able to perform normal swimming movements and gave indications of ability to see. In some instances they lived for over a month (Stockard, '10a). Paolucci ('74), however, described a cyclopean ray (fig. 3), caught in the Adriatic, which measured 20 cm. to the base of the caudal fin. The mouth was well-formed and any brain anomalies (not described) which may have existed were apparently relatively unimportant as far as the animal's ability to survive so long was concerned.

II. EXPERIMENTAL PRODUCTION OF CYCLOPEAN MONSTERS

The hope of one day attaining an adequate understanding of cyclopia is considerably strengthened by two important considerations, first the fact that the anomaly may be experimentally produced with considerable ease, and secondly, the fact that experimentally produced cyclopean monsters exhibit essentially the same features as those 'spontaneously' arising.

Aside from some preliminary experiments of Geoffroy St. Hilaire's, Dareste ('77) was the first to undertake systematically the experimental production of developmental anomalies. By incubating eggs in a vertical position, the use of abnormal temperatures, varnishing the shell with substances impermeable to air, and unequal warming of the eggs, he was able to produce "several thousand" monstrous chicks, among which were some exhibiting various degrees of cyclopia. Féré ('00, p. 796) also obtained cyclopean chicks from eggs subjected to relatively high temperatures before incubation. *Fundulus* eggs reared for a short time after fertilization in subnormal temperatures may also give rise to cyclopean monsters or other eye defects (Kellicott, '16; Loeb, '15).

The production of cyclopia by the use of chemicals has been highly successful. This was first accomplished by Stockard ('07–'10) in his now classical experiments on *Fundulus* embryos treated with varied strengths of $MgCl_2$, $MgCl_2$ + NaCl, $Mg(NO_3)_2$, and $Mg(NO_3)_2$ + NaCl. Alcohol, ether, chloroform and chloretone were also used, alcohol being most effective; at times as many as 90 per cent of the embryos treated with a 3 per cent solution were eyeless, asymmetrically monophthalmic, or cyclopean ('10a, p. 371). His experiments further show that the action of chemicals must be exerted relatively early since eggs treated later than 15 hours after fertilization failed to respond, the most effective period being the 8–32 cell stage. Cyclopean fish embryos were subsequently produced in variable numbers by the use of NaCl, LiCl, NaOH, amyl alcohol, acetone (McClendon, '12a), and butyric alcohol (Werber, '16a, b).

Cyclopean amphibian embryos have been produced by treating the eggs in early stages of gastrulation with lithium chloride, ethyl alcohol, chloralhydrate (*Rana*, *Triton*, LePlat, '13, '14, '19; *Rana* and *Triton*, Cotronei, '22a, b; *Rana*, Guareschi, '34; *Amblystoma*, Adelmann, '34), phenol and chloretone (*Triton*, Lehmann, '33). The exposure of incubating eggs of the fowl to alcohol vapors is productive of a small percentage of cyclopean monsters (Féré, '99; Stockard, '14).

Cyclopia has also been produced by mechanical interference. The experiments of Spemann ('01 b, '02, '03 a, '04) are of special interest in this connection. By constricting the egg of *Triton* with a hair loop in stages ranging from the two-cell to early gastrulation stages, double headed monsters were produced (fig. 9). If the ligature was oblique, the component related to the smaller segment of the blastopore was small and often cyclopic. When the constriction was less pronounced

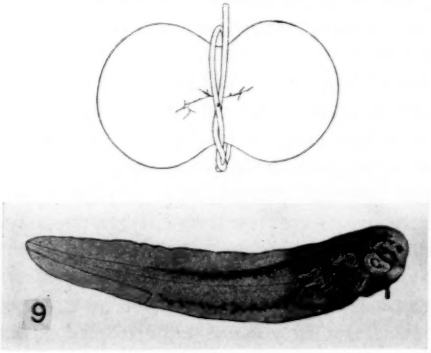


FIG. 9. LARVA OF TRITON TAENIATUS (BELOW) ELEVEN DAYS AFTER OBLIQUE CONSTRICTION OF THE EARLY GASTRULA (ABOVE)

The constriction of the gastrula results in incomplete doubling of the head of the larva, the left side of which is normal, the right cyclopean. Only the right eye of the left head can be seen in the figure. On the right side the single cyclopean eye, the single olfactory pit lying above it and the closely approximated balancers are shown. (From Spemann, '04).

three-eyed monsters might result, the middle eye being shared by the two incompletely separated heads and one case of partial fusion of four eyes is described. By pricking the anterior end of the embryonic shield of *Fundulus*, Lewis ('09) obtained some typical cyclopean specimens. Especially interesting, however, is the experiment of Mangold ('31) who was able to produce the anomaly by the removal of the anterior portion of the roof of the archenteron of *Triton*. (Fig. 10).

Attempts to 'Explain' Cyclopia

The greatest diversity of opinion has existed as to the cause of cyclopia. This is, no doubt, partly due to the failure on the part of some to appreciate the fact that a number of very diverse factors may evoke essentially the same morphogenetic response; partly to an imperfect knowledge of the exact nature of the physico-chemical or mechanical alterations of cells produced by alteration of environmental conditions and their expression in morphogenetic terms; and also, in large part, to the incompleteness of our knowledge of normal developmental processes, a condition which has now been, at least partially, remedied by experimental work, notably by Spemann and his school.

We may at once eliminate maternal impressions from the list of possible 'causes' which have been advanced to account for the anomaly. Dareste ('77, '91) and others have regarded cyclopia as due to amniotic compression leading to an arrest in the development of the anterior cerebral vesicle. Although there is evidence that the anomalous formation of the amnion, dating from the earliest stages of development, is sometimes associated with malformations (Streeter, '30), the fact that cyclopia is common among the anamniota and that no confirmatory evidence of its rôle in the production of the anomaly in the amniota exists, indicates that we may eliminate this factor, also, as a causative agent, at least in the vast majority of cases.

The Nature of the Action of Physical and Chemical Agents

We are still ignorant of the exact nature of the effects of chemical and thermal alterations of the environment. Stockard ('10a) at first believed that eye anomalies "all of which are more or less arrested

conditions of development, result from anaesthesia during development", but McClendon ('12a) obtained similar results with NaCl, $LiCl_2$ and NaOH "to which an opposite effect is rather to be ascribed". Finding the order of effectiveness of kations in producing cyclopia to be Mg < Li < Na, he supposed their action to be physico-chemical. The degree of toxicity (McClendon, '12b) is apparently not important, solutions of equal toxicity showing striking differences in the effects of different substances. Werber ('16a, b) believes that various solutions produce a chemical lesion (Blastolysis) so altering the cells chemically as to render those affected incapable of the reactions necessary for normal development. LePlat ('19) in his judicious summary of the subject concludes that "there is no specific teratogenetic substance, that numerous toxic agents modify development, very probably by action on the nuclei, and that it is the stage during which the agent

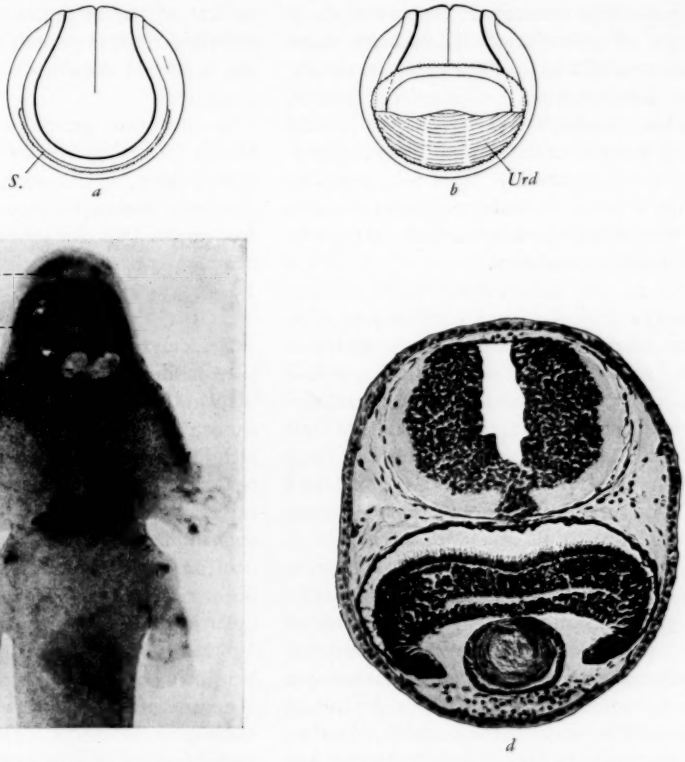


FIG. 10. PRODUCTION OF SYNOPHTHALMIA AND CYCLOPIA IN THE EARLY NEURULA OF TRITON

Figures *a* and *b* are schemas showing the operation which consists of cutting around the cephalic fourth of the medullary plate peripheral to the neural ridge, flapping back the medullary plate, and removing the underlying roof of the archenteron. Figure *c* shows the embryo ten days after the operation. Figure *d* is a section through the head showing an almost completely single eye with a single lens. (From Mangold, '31.)

has actively influenced the development of the egg which has provoked the differences in the observed results". The same solutions produce a graded series of anomalies. Thus, a .5 per cent solution of $LiCl_2$ acting upon young blastulae of *Rana* results in abnormal gastrulae with largely open blastopores. In the early stages of gastrulation it produces asyntaxia medullaris, cauda bifida, anencephaly, anophthalmia, rudimentary brains, nanism, hydrops and paralysis. Acting upon more advanced gastrulae cyclopia is the most commonly observed anomaly, while later on the embryo grows incapable of withstanding such marked changes in environment and dies.

As to the observable effects of low temperatures Kellicott ('16) states that they consist in inequality in the distribution and combinations of both nuclear and cytoplasmic substances, and in disturbances in the formation of the cell walls. "The cause of abnormal and monstrous development . . . is to be found in a disturbance of the normal organization of the ovum."

The evidence as a whole, therefore, seems to indicate that there is no specific agent responsible for the production of cyclopia, that a variety of abnormal environmental influences may produce a graded series of abnormalities depending upon the severity of their action, the time of development during which they act and the vigor of the individual. All things considered, the most active tissue at the time will be most seriously affected, and upon what parts of the embryo are affected will depend the subsequent course of development as a result of the initiation of a series of abnormal developmental interactions. This, in a general way, is in conformity with the theory of differential susceptibility advanced by Child ('20, '21, '28) in connection with the theory of axial gradients. Any specificity which exists will, therefore, as LePlat ('19) and Stockard ('21) point out, be related rather to the period of development during which the inhibitory agent exerts its influence than to any specific action of the same. For a more thorough review of the evidence concerning these so-called critical periods of development, the work of Needham ('31) should be consulted.

In the same general category belongs Mall's ('08, '17) theory that nutritional disturbances, occasioned, in the case of placental forms, by faulty implantation, are responsible for anomalous development.

The Rôle of Genetic Factors

Defects of the germ plasm have also been held to be a possible agent, notably by Wilder ('08) and there is evidence to show that this may be true in some cases, although the evidence seems to indicate that in most instances environmental, rather than hereditary factors, are responsible (Stockard, '10). In this connection we may note that cyclopia has been recorded as occurring in siblings (van Duyse, '09; Klopstock, '21; Mall, '17) but we must recognize that a germinal origin is not thereby proved since we are ignorant of environmental conditions obtaining in the uterus. However, that germinal factors may sometimes be involved is clear from the work of Loeb ('15) who was able by hybridization to produce eye defects in *Fundulus*. Further evidence is adduced by Wright and Wagner ('34) who have studied a series of over 300 monstrous guinea pigs descended by brother-sister mating from a single mating made in 1906. Most of these are otocephalic and many are, in addition, cyclopic. They conclude that both environmental and hereditary factors take part and sug-

gest that the latter are the ones which bring about a general inhibition to which the momentarily most active regions of the embryo are susceptible. "Whether the genes have a directly depressive action at the critical moment or whether they produce such an increase in activity as to bring about susceptibility to trivial environmental conditions is a question to which no answer can be given at present."

Morphogenetic Interpretations

On the morphogenetic side most of the attempts to explain cyclopia have centered in the interpretation of the origin and nature of the early eye anlagen. Speer (1819) and Meckel (1826) interpreted the anomaly as due to the more or less perfect fusion of two originally separate eyes and the concomitant malformations of the head were likewise interpreted on the basis of simple fusion of separate parts. On the other hand, Huschke (1832) from his study of the early development of the chick concluded that the two eyes are represented early in development by a single vesicle situated anterior to the brain which subsequently grows forward to effect a subdivision of the originally single optic anlage into two optic vesicles. Cyclopia was interpreted as a developmental arrest. Some external factor operating early in development was thought to simultaneously inhibit the further evolution of the brain and eye, and these in turn when they remained single would constitute the causal factor for associated malformations of the skeleton and musculature.

It may be stated at once that in its original form neither of these explanations is any longer tenable. While more or less complete fusion of optic cups or vesicles has been experimentally effected (Born, '97, pp. 537 ff.; Anastasi, '13; Pasquini, 1927a, p. 74, 1927b, 1929a, p. 100, 1929b, p. 264; Truniger, '27; Detwiler, '29) modern workers are agreed that no crude fusion of already formed optic vesicles can be demonstrated as occurring, at least in experimental cyclopia (Spemann, '04, '12b; Stockard, '09b). Huschke, as Dareste ('77) points out, obviously confused the entire prosencephalon with the optic vesicles which are in all vertebrates normally paired when they first push out from the walls of the forebrain, a fact clearly established by von Baer (1828, pp. 23–24). It is interesting to note, however, that von Kupffer's ('90) description of an originally single optic vesicle in *Petromyzon* was only recently refuted by Keibel ('28).

Although discredited in their original form, the interpretations of Meckel and Huschke survive in altered form in two opposing points of view of more modern workers. The fact that the cyclopean eye is single from its first appearance does not preclude the possible fusion of two prospective anlagen in earlier stages of development, nor the possibility of a primitive potentially single anlage which subsequently becomes separated into two parts with the expansion of the optic vesicles. This furnishes the basis for two opposing schools of thought at the present time.

Dareste ('77, '91) advocated the fusion of separate optic anlagen attendant upon a developmental arrest which delayed the closure of the anterior neuropore and inhibited the forward growth and bilateral expansion of the prosencephalon. The parts destined to form the optic vesicles consequently fuse and form a single evagination anterior to the foregut. Pressure of the amnion was supposed to be the inciting factor.

Spemann is the leading contemporary advocate of this view that two separate

and distinct optic anlagen are normally determined in the early neural plate. His thoughtfully conceived and beautifully executed experiments on *Rana*, *Bombinator* and *Triton* (Spemann, '01b, '03a, '04, '12b) have convinced him that there exists in the early neural plate stage a complete and rigidly determined mosaic of all the parts of the future cyclopean or normal eye. The visual and pigment layers of the retina, the optic stalk and chiasma all occupy definite areas of the neural plate and are unable to substitute for one another when one or the other is rendered defective or is lacking, as after puncture of the anterior end of the neural plate with a hot needle (Spemann, '01a, '03b). Each differentiates strictly in accordance with its prospective significance when transplanted (Spemann, '12a) or displaced by rotation of a rectangular area of the anterior end of the neural plate (Spemann, '12b). This experiment (fig. 11) consisted in the rotation through 180° of a rectangular area of the anterior end of the neural plate together with the underlying roof of the archenteron. If the anterior end of the excised piece passed through the eye anlagen, four eyes were developed in the embryo after healing, two from those portions of the optic mosaic remaining in situ and two from the caudally displaced portions. The right posterior and left anterior eyes, and vice versa, supplemented one another qualitatively and quantitatively, the parts lacking or

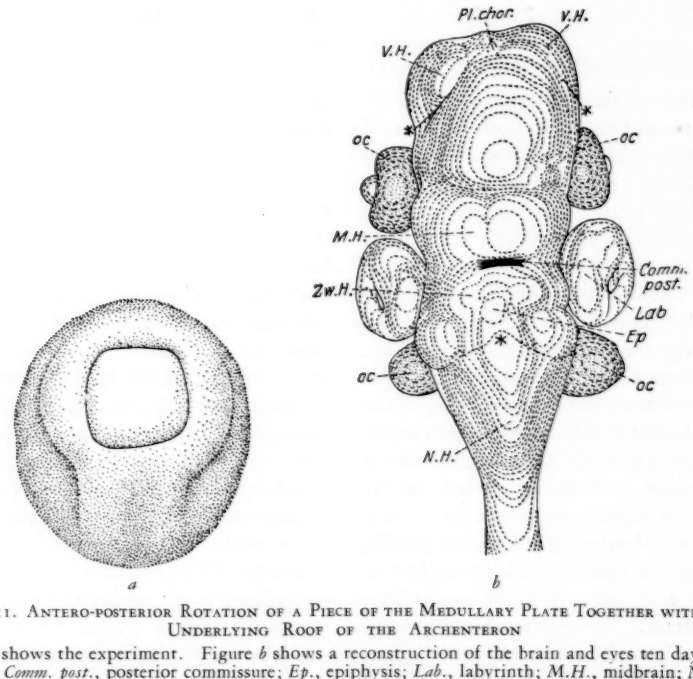


FIG. 11. ANTERO-POSTERIOR ROTATION OF A PIECE OF THE MEDULLARY PLATE TOGETHER WITH THE UNDERLYING ROOF OF THE ARCHENTERON

Figure *a* shows the experiment. Figure *b* shows a reconstruction of the brain and eyes ten days after the operation. *Comm. post.*, posterior commissure; *Ep.*, epiphysis; *Lab.*, labyrinth; *M.H.*, midbrain; *N.H.*, hindbrain; *oc.*, optic cup; *Pl.Chor.*, choroid plexus; *V.H.*, forebrain; *Zw.H.*, diencephalon. The line marked with an asterisk shows the line of fusion. (From Mangold, '28, after Spemann, '12b).

underdeveloped in one being represented in the other. A caudally displaced tapetal vesicle was for example matched by a well developed eye formed on the opposite side in its normal location. As a result of his constriction experiments, previously referred to, he concluded that the cyclopean eye is likewise represented in the neural plate by a mosaic of rigidly determined parts, in this case the single median primordium having arisen by the fusion of more laterally situated parts due to the absence or deficiency of median regions of the neural plate. Fischel ('21) has adopted Spemann's conception in his study of cyclopean *Salamandra* embryos and attempted to reconstruct the arrangement in the neural plate of the parts of the optic mosaic of both normal and cyclopean eyes by following back into it the various parts of the optic cup. His diagrams (fig. 12) illustrate the essential features of this point of view which has received further experimental support from King ('05) and from Lewis ('07, '09) who was able to produce typical cyclopia in *Fundulus* by injury of the anterior end of the neural plate with a heated needle. It has also been adopted by many subsequent writers (e.g. Mall, '17; Seefelder, '08, '30; Cotronei, '22; Tsuda, '24; v. Querner, '25; *et al.*).

The opposing view that the two eyes are represented in the neural plate by a single median zone of eye-forming material finds its champion in Stockard, who as the result of his studies on cyclopean *Fundulus* monsters (Stockard, '09b) and excision experiments on *Amblystoma* (Stockard, '13a, b) concluded that the

> eye anlage in the medullary plate is primarily median and single and normally separates into two almost equal growth regions which develop in lateral directions reaching further and further out until finally the optic vesicles come into contact with the ectoderm ('13b, p. 254). There is no medullary material between the eye anlagen. The median tissue is the eye anlage itself and will subsequently go to form some portion of the eye, either optic cup or optic stalk, depending upon its position and the extent of normal development attained (p. 269). In . . . cyclopia . . . the median eye anlage does not widen or spread laterally but is arrested in its primary condition; thus the two growth centers are not sufficiently separated and only a single optic center exists . . . (p. 273).

Essentially similar to Stockard's interpretation is that of LePlat ('19) who introduced the convenient term "optico-ocular apparatus" which includes all of the structures—the optic vesicles, optic stalks and primary optic chiasma—which develop from the "simple median anlage precociously formed in the medullary plate" (fig. 13).

A third interpretation has been developed by Rabaud ('01, '02) who studied a large number of cyclopean chick embryos. His position is difficult to understand but in essence he maintains that the developmental processes underlying the formation of the cyclopean head have no analogy in normal development. The neural plate remains flat for a long time and is subsequently closed by a sort of epiboly of the cells at its margins. The simple cyclopean eye arises not by a fusion of separate anlagen but as a result of a more or less complete "indivision" of a common anlage. His interpretation in this latter respect is therefore somewhat closely related to that of Stockard. As Schwalbe and Josephy ('13, p. 245) point out it is likely that Rabaud was dealing with anencephaly rather than cyclopia proper for no comparable delay in the closure of the neural folds has been described in other forms.

It will be clear that, aside from the possibility that the cyclopean eye is a structure arising by processes finding no parallel in normal development, its explanation in morphogenetic terms will depend upon whether the first or second

of the above interpretations is accepted. If the optic anlagen are regarded as double and separated by medullary tissue, the cyclopean eye can arise only when the median region is defective or lacking. On the other hand, if the material for the eyes is present in the neural plate as a median group of cells which subsequently spreads laterally to give rise to two eyes, cyclopia will be interpreted as an arrest in eye formation. The median group of eye-forming cells in case its bilateral

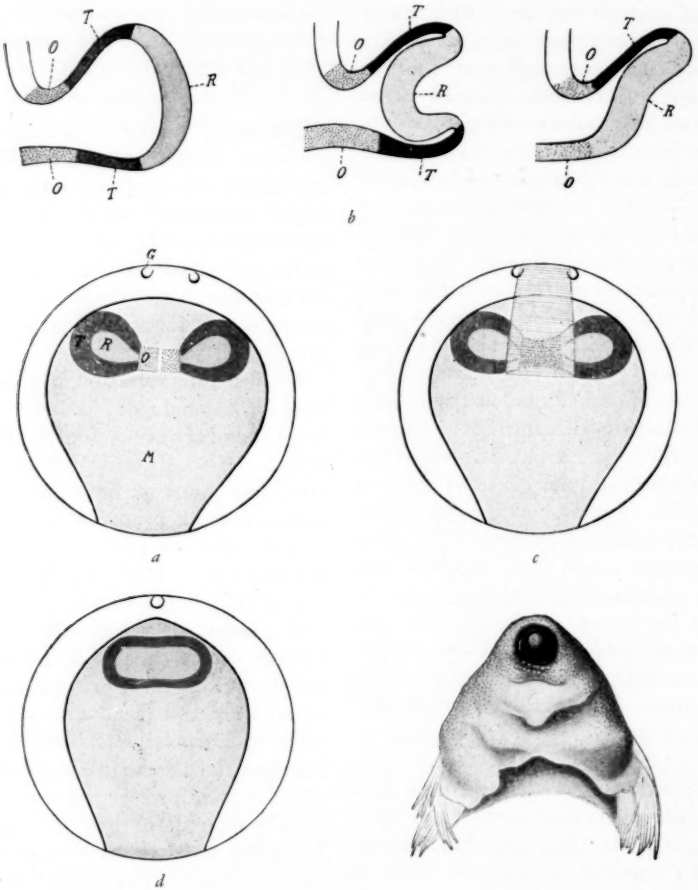


FIG. 12. (A) THE NORMAL TOPOGRAPHY OF THE EYE-FORMING MATERIALS OF THE NEURAL PLATE ACCORDING TO FISCHEL ('21). (B) SCHEMATIC TRANSECTIONS OF THE NORMAL OPTIC VESICLE AND CUP, SHOWING THE UTILIZATION OF THE REGIONS MAPPED OUT IN (A). (C) DIAGRAM SHOWING THE EXTENT OF THE MEDIAN 'DEFECT' IN CYCLOPIA PERFECTA. (D) THE ARRANGEMENT OF EYE-FORMING MATERIALS IN CYCLOPIA PERFECTA. (E) VENTRAL VIEW OF HEAD OF LARVA OF SALAMANDRA ATRA EXHIBITING CYCLOPIA PERFECTA. (FROM FISCHEL, '21).

G., olfactory pit; *M.*, medullary plate; *O.*, optic stalk; *R.*, retina; *T.*, pigment layer of retina.

expansion is checked must be thought capable of differentiating harmoniously into a single cyclopean eye.

While, as we shall have occasion to point out, both interpretations have a large element of truth and the results of the experiments performed are perfectly valid under the conditions imposed, later work has served to show that a reinterpretation is probably necessary. A number of objections to each in its original form immediately come to mind. (1) Thus in attempting to schematize the Spemann interpretation Fischel ('21) has represented the materials for the optic stalk and chiasma as being confined to a narrow median region of the neural plate, but Petersen ('23) has pointed out the incorrectness of this assumption. It is clear that when projected into the neural plate the material for the optic stalks would form a complete ring around the tapetum region on both sides, as illustrated in figure 14 and would not be confined to median territory as Fischel's diagrams indicate. A purely median defect would therefore not lead to an entire lack of optic stalk material and it is, moreover, difficult to conceive what circumstances would lead to a strictly localized bilateral deficiency of these rings of prospective optic stalk cells resulting in the absence of optic stalk and chiasma observed in many cases of cyclopia. (2) The fact that imperfect eyes may develop after puncture of the neural plate by a heated needle (Spemann, '01a, '03b) and that eyes lacking tapetum or retina may in some cases develop from transplanted fragments of the neural plate (Lewis, '07; Spemann, '12a) does not positively prove that the cells are not equipotential to a certain degree. Altered conditions of development (as when the eye comes to lie in the coelom) may have prevented a full expression of potencies. In some cases possibly too small a fragment has been transplanted. There is furthermore no exact knowledge of what cells have been damaged or removed in these experiments and the lack of parts must be explained by the assumption that certain cells have been destroyed or not transplanted. (3) Recent experiments (Adelmann, '29a, b; Mangold, '31, p. 222), as will subsequently be noted, indicate that the prospective eye-forming territories are not sharply delimited in their potencies. (4) Finally the experiments performed in support of both interpretations were carried out and interpreted without

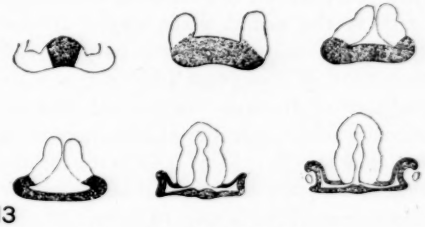


FIG. 13. A SERIES OF DIAGRAMS ILLUSTRATING THE CONCEPTION OF LEPLAT

The single median 'optico-ocular' anlage of the neural plate stage is represented as expanding to form both eyes and the intervening material of the floor of the brain in the region of the primitive chiasma. (From LePlat, '19).

reckoning on the influence of the roof of the archenteron which Spemann ('24, '31), Marx ('25), Mangold ('33) and other workers have subsequently shown to exercise such a profound influence on the determination not only of the eye but of the neural plate in general.

III. THE PROSPECTIVE SIGNIFICANCE AND PROSPECTIVE POTENCIES OF THE NORMAL OPTIC ANLAGEN

It will be evident that in attempting to derive an explanation of cyclopia from the normal disposition and characteristics of the eye-forming materials of early stages, two aspects of the problem—the

prospective significance and the prospective potencies of the cell groups—should always be clearly delimited. The former is a purely morphological concept dealing with the normal fate of definite cells, cell groups or aggregates. Prospective potency is a physiological one, taking into account the adaptive or regulative capacities of cell groups. The problem of cyclopia is primarily a physiological one, involving the atypical utilization of cells or cell groups and is thus intimately concerned with the problem of prospective potency. In the Spemann interpretation prospective significance and potency are held to coincide from a period at least as early as the neural plate stage. In cyclopia the cells participate only in the formation of structures they would normally have formed. The single median eye arises through the elimination of a region normally utilized only in the formation of the optic stalks and chiasma which this region alone is able to form. In the Stockard interpretation, the prospective significance of the cell aggregates in cyclopia is different from the normal. A median group of cells normally utilized in the formation of the optic stalks or chiasma forms tapetum or retina. The potencies of these cells are therefore greater than their prospective significance, and changed conditions awaken latent potentialities not normally expressed.

Further, in speaking of determination it is necessary to be careful to define terms and state exactly the conditions under which a determination of parts is supposed to have occurred. As Harrison ('33) has so clearly pointed out "trouble begins when . . . we use the word to denote a state and ask the question whether an organ rudiment is 'determined' or not; meaning thereby whether it is so fixed as to its capacities that it can do but the one thing that it does do." It is a fact, well known to experimental embryologists, that an isolated part tends to form a greater number and variety of structures than when left in situ (Lewis, '10; Kusche, '29; Bautzman, '29; *et al.*) and that furthermore the expression of more or less generalized potencies may be profoundly altered by secondary factors in the environment (Holtfreter, '29, '34).

The Eye Anlage

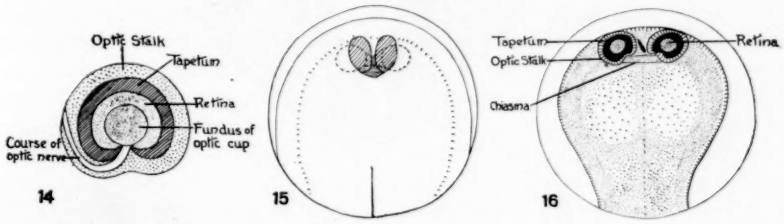
Returning to the interpretation of cyclopia on an embryological basis, the first task therefore is to determine the prospective significance and the prospective potencies of the eye-forming materials of the normal embryo and the factors influencing the normal expression of these potencies. The use of vital dyes in the study of the prospective significance or fate of various regions of the egg was introduced by Goodale ('11) but the technique was greatly improved by Vogt ('25, '29) with so much success that the mapping of various regions of the egg and embryo has proceeded apace. The method of Vogt consists in brief in the application of thin pieces of agar, previously stained with nile blue sulphate or neutral red, to the surface cells which absorb, retain and confine the stain in well localized areas. Vogt ('25, '29) has determined the site of the presumptive eye anlage in the early gastrula stage of urodeles and anura. In the former it lies in the region of the animal pole, in the latter about 40° to 50° above the equator. Vogt's method has been recently employed by Manchot ('29) and Woerdeman ('29) to study the prospective significance of the eye-forming regions of the neural plate. Their schemas, based on the results of their experiments, are reproduced in figures 15 and 16. Manchot, who used *Amblystoma tigrinum*, *Pleurodeles* and *Triton*, concluded that in the early neurula, when the

boundaries of the medullary plate are indicated by a mere pigment line, the eye anlage occupies a region corresponding in length and width to one-fourth to one-third of the greatest breadth of the neural plate, its anterior boundary encroaching upon the anterior neural ridge. During the elevation of the neural folds the eye material is drawn out and shortened in a sagittal direction and the lateral parts displaced forward somewhat so that when the neural folds have appeared, the material occupies about one-half the breadth of the neural plate and is eventually evaginated to form the optic vesicles. The materials for the two eyes are separated in the midline only by a narrow wedge of material which forms the basal portion of the lamina terminalis and chiasma. Immediately back of this wedge, continuity across the midline is effected by the materials for the optic stalk and chiasma. "If one considers the stalk material as part of the eye anlage, which according to its development appears logical, there actually exists from the first a single anlage-territory for the two eyes connected posteriorly and having an original extent closely agreeing with the statements of Stockard."

Woerdeman agrees in a general way with Manchot but insists that even in the early gastrula there lies between the two eye plates (Augenplatten) a group of cells which becomes the chiasma region. This expands laterally, but

> that is something quite different from what Stockard thought; he assumed a median cell group in the neural plate, which grows out to both sides and separates into one anlage for the left and one for the right eye. . . . In opposition to this conception, I can show that such an outgrowth does not occur, that only the territory in the midline extends in a lateral direction, but that the cell groups from which the right and left eyes arise are already in the gastrula separated from one another by material of other prospective significance.

The close agreement between the schemas of Petersen ('23) and Woerdeman ('29) is at once apparent. Disregarding slight differences in the results of Manchot and Woerdeman, it is clear, then, that the prospective significance of a narrow median group of cells is to form the primitive chiasma region (a narrow zone in the region of the primitive optic furrow) and a part of the optic stalks. However, the question of the prospective potencies of the various portions of the eye-forming territories (optico-ocular apparatus) is still open.



FIGS. 14–16. THE SCHEMA OF PETERSEN (FIG. 14) SHOWING THE PRESUMPTIVE SIGNIFICANCE OF THE PARTS OF THE OPTIC ANLAGEN IN THE NEURAL PLATE CONTRASTED WITH THOSE OF MANCHOT (FIG. 15) AND WOERDEMAN (FIG. 16) WHICH WERE CONSTRUCTED FROM OBSERVATIONS OF VITALLY STAINED EMBRYOS.

The Indifference of the Presumptive Ectoderm of the Early Gastrula

In the last fifteen years much information has been added concerning the factors influencing the release or the expression of

the inherent potencies of cells and cell groups during development. Spemann ('18, '21) has demonstrated that the entire presumptive ectoderm of the early gastrula is to a certain extent 'indifferent' or plastic and that the fate of any particular region of it depends largely upon its relations to the whole organism. Thus when the presumptive belly epidermis of *Triton cristatus* and the presumptive neural plate of *Triton taeniatus* are exchanged (fig. 17) the former, coming to lie in the anterior end of the neural plate of the host, participates in the formation of the eye and

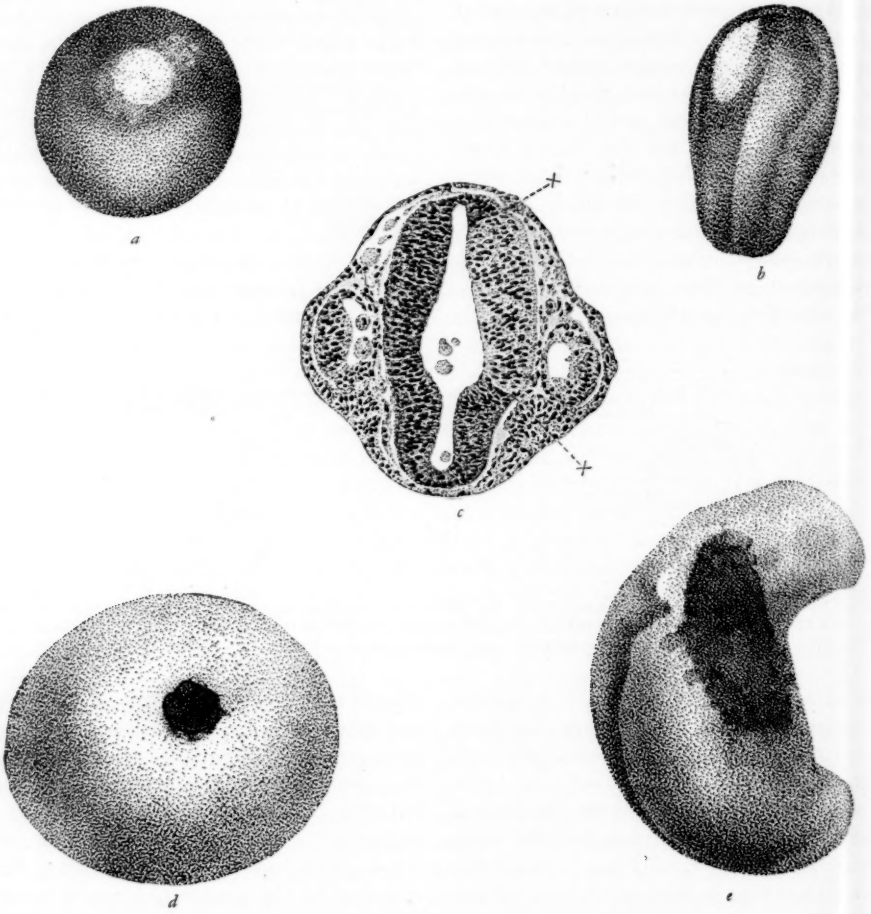


FIG. 17. EXCHANGE OF A PIECE OF PRESUMPTIVE MEDULLARY PLATE AND EPIDERMIS IN THE GASTRULA STAGES OF TRITON TAENIATUS (A–C) AND TRITON CRISTATUS (D, E).

The presumptive belly ectoderm of *cristatus* forms part of the neural plate (*b*) and brain (*c*) of *taeniatus*. The presumptive neural plate of *taeniatus* forms epidermis in *cristatus* (*e*). (From Mangold, '31, after Spemann).

neural tube; the latter forms epidermis. Presumptive ectoderm may, in fact, yield mesodermal structures under certain conditions (Mangold, '23). The fate of these tissues is obviously controlled by some factor, not species-specific, resident in their organismic environment. Holtfreter ('34) has recently demonstrated the same fact in an equally striking fashion. Presumptive epidermis and prospective neural plate when cultured in physiological salt solution both yield irregular masses of epidermal cells. In the early gastrula stage the entire ectoderm represents a homogeneous, harmoniously equipotential system which requires for differentiation in accordance with its presumptive significance (herkunftsgemäss) certain external factors not offered by this particular culture medium. When reared in a coelomic sac, however, (Holtfreter, '29) presumptive medullary plate may differentiate into typical nervous tissue. It has also been shown that in the developing organism the differentiation of the nervous system normally proceeds under the influence of the roof of the archenteron or the dorsal regions of the marginal zone of the blastula or gastrula from which it is derived (Spemann and Mangold, '24, '31; Bautzmann, '26; Marx, '25; Lehmann, '26, Mangold, '33; *et al.*). Holtfreter ('33a) has demonstrated the same effect in tissue cultures. A large piece of gastrula ectoderm of *Triton alpestris* (presumptive epidermis or medullary plate) was combined in a medium of physiological salt solution with an isolated piece from the dorsal marginal zone (presumptive roof of archenteron) of *Triton alpestris*. The pieces were broken into small fragments and mixed together. In this case, under the influence of the materials of the marginal zone which differentiates into notochord, muscular tissue and pharyngeal epithelium, the prospective ectoderm has differentiated into neural tube. Holtfreter concludes that these induction effects obtained in explants confirm the conclusion reached by other workers that the origin of the entire nervous system and the sense organs is dependent upon its being underlain by the derivatives of the dorsal marginal zone of the gastrula. In accordance with these results it is not surprising to find that the eye anlage also depends for the localization and the expression of its potencies upon some influence exerted by the roof of the archenteron.

The Localization of Eye-forming Potencies

In attempting to determine the time when these eye-forming potencies are first localized in the region of the anterior end of the neural plate, Mangold ('28) transplanted from various species of *Triton* in different stages of gastrulation the presumptive brain and eye anlage without the roof of the archenteron into the blastocoele of young gastrulae. The youngest transplant which yielded an eye was derived from a donor with a medium sized yolk plug. It had been completely underlain by the roof of the archenteron at the time of transplantation (fig. 18). The frequency with which eyes were differentiated from the transplants increased in older stages so that Mangold concludes that before the neurula stage no definite localization of eye-forming potencies exists, a definitive localization being established only in the early neurula stage. From the experiments of Stockard ('10a), Werber ('16a, b), and Hoadley ('28) on *Fundulus*, Mangold ('31) suggests that in this form also determination of the eyes occurs during the formation of the embryonic disc and is definitive by the time the "narrow" embryonic disc has appeared. Hoadley ('26) found that in transplants of the early blastoderm of the

chick onto the chorio-allantoic membrane, the first eyes were encountered in transplants from blastoderms which possessed a broad primitive streak and which had been incubated about 4 hours before transplantation. However, the eyes differentiated from these earliest blastoderms were imperfect, a progressive improvement in the quality of differentiation occurring in transplants from later stages. The localization of eye-forming potencies in the chick evidently begins therefore during the primitive streak stage, and becomes more and more stable until the head process stage when the potencies are more or less fixed. Further details will be found in Mangold's ('31) exhaustive review.

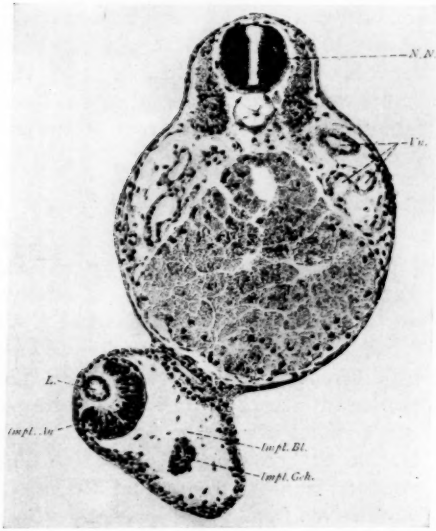


FIG. 18. SECTION OF A TRITON EMBRYO, SEVEN DAYS AFTER A PIECE OF PRESUMPTIVE BRAIN AND EYE FROM A GASTRULA OF TRITON ALPESTRIS WITH A MEDIUM-SIZED YOLK PLUG HAD BEEN TRANSPLANTED WITHOUT THE UNDERLYING ROOF OF THE ARCHENTERON INTO THE BLASTOCOELE OF THE HOST.

The implant has differentiated into a well-differentiated eye which has induced the formation of a lens. *L.*, lens; *Imp. Au.*, well-differentiated eye of implant; *Impl. Bl.*, ectodermal vesicle of host evoked by the implant; *Impl. Geh.*, 'shaved' portion of implanted brain; *N.H.*, neural tube of host; *Vn.*, pronephros. (From Mangold, '28.)

We may next inquire into the nature and localization of the factors responsible for the localization (or segregation) of eye-forming potencies and their expression in the differentiated eye. Mangold ('31) suggests that the localization or segregation of eye-forming potencies may be brought about in three possible ways: (1) through the influence of the entire organism, (2) through factors arising in the anlage itself during the course of development, and (3) through factors in the neighboring regions of the egg. For a discussion of the first two possibilities for which there is some evidence the reader must, for lack of space, be referred to Mangold.

The third possibility, the influence of factors residing in neighboring parts, recalls the influence of the roof of the archenteron on the differentiation of the nervous system. From the work of Spemann ('31), Holtfreter ('33a, d). Mangold ('31), *et al.* there seems to be little doubt that the localization of eye-forming potencies normally proceeds at least largely under the influence of the prechordal region of the roof of the archenteron or the dorsal portion of the marginal zone. The latter, in early gastrula stages, lies at the dorsal lip of the blastopore and since it is the first portion of the marginal zone to be invaginated moves forward under the ectoderm until it finally comes to lie under the anterior end of the prospective neural plate. The dorsal lip of the blastopore of the early gastrula transplanted to an indifferent region of the host induces a head with normally proportioned eyes. Spemann ('31) and Holtfreter ('33a, '33c) have demonstrated in the clearest fashion a regional polarization of the materials of the marginal zone

along its prospective antero-posterior axis. That a comparable qualitative difference in the inductive capacities of the roof and described in figure 19. Further confirmation of the facts here briefly mentioned will be given subsequently.

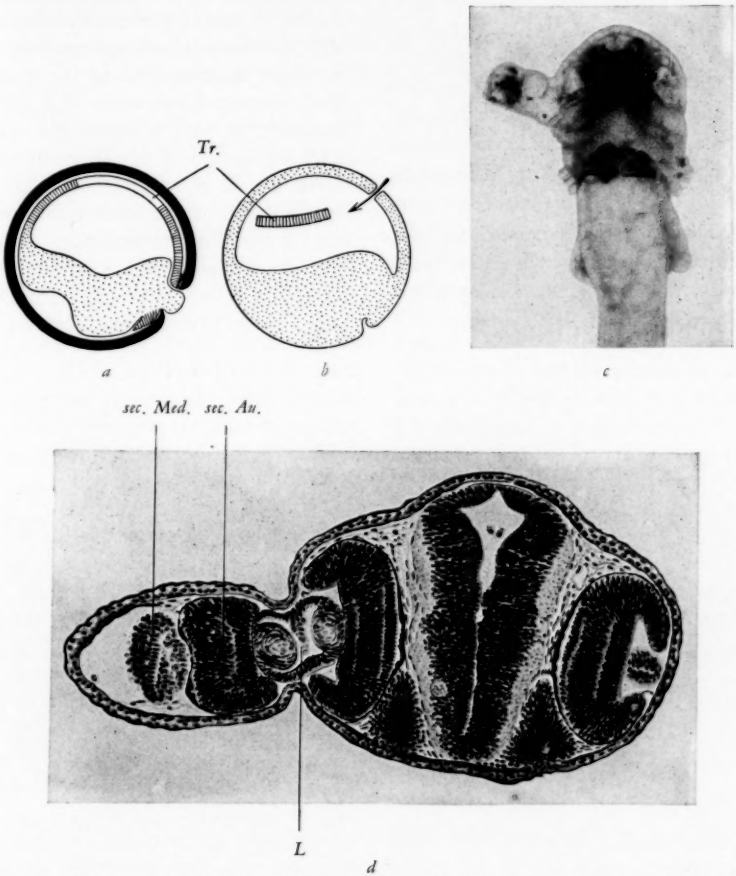


FIG. 19. THE INDUCTION OF AN EYE BY TRANSPLANTED ROOF OF THE ARCHENTERON OF TRITON

The operation is schematically shown in (*a*) and (*b*). A piece of the roof of the archenteron of a gastrula possessing a small yolk plug is implanted in the blastocoele of an earlier gastrula. (*c*) Ventral aspect of the host some days after the operation showing a large protuberance in the vicinity of the right eye. (*d*) Transection through the head of the same. The protuberance contains a small piece of medullary tissue and a well differentiated eye whose lens is fused with that of the host. (From Mangold '31, after Spemann).

of the archenteron exists is clear from the work of Spemann, Holtfreter, and Mangold ('33). One especially interesting experiment of Spemann's is illustrated

There is also evidence that inducing factors exist in the medullary plate itself. The transplantation of a piece of medullary plate from the presumptive eye region of a

Urodele into the blastocoele of another embryo in an early stage of gastrulation leads to the induction of a secondary brain and eye (Mangold and Spemann, '27; Mangold, '29, '29a, '32, '33). A piece of medullary fold together with some adjacent epidermis from the early neurula which would normally form some brain, olfactory placode and epidermis but no eye, may induce brain and eye when transplanted into the blastocoele (Mangold, '31). In the case of the medullary plate also a qualitative difference in its inductive capacities along its antero-posterior axis exists (Mangold, '33).

It has been possible in the preceding discussion to sketch only in the barest outline certain aspects of the induction problem, for a fuller discussion of which the reader must be referred to the voluminous literature which now exists, a guide to which is contained in the few works cited above. From what has been said, however, it will be clear that normally the localization of eye-forming potencies in the neural plate proceeds largely under the influence of the prechordal portion of the roof of the archenteron. The situation is complicated, however, by the possible action of adjuvant factors resident in the neural plate, or the 'egg as a whole'.

MORPHOGENESIS OF THE SHOULDER ARCHITECTURE

PART IV. REPTILIA

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IN THE present contribution to the morphology of the shoulder architecture the reptilian stage will be discussed. This involves consideration of pertinent features of the skeleton of Permian and Triassic representatives of the orders Cotylosauria and Theromorpha, as well as mention of a few other fossil forms. As a basis for extended discussion of the skeleton and soft parts the lacertilian *Iguana* has been selected for the reason that live material in required quantity could be secured. Comparisons are drawn with the more significant features of *Cyclura*, and of *Uromastix* where these differ, and with the dissections of the rhynchocephalian *Sphenodon* as reported in the literature. Without live material it was thought needless to dissect the latter, as the work on it already published is of excellent quality. For the loan of both skeletal and spirit specimens of lacertilians I am indebted to the U. S. National Museum.

In any such anatomical study as the present it is necessary constantly to bear in mind the mechanics of the type of body movements employed and the position in which the parts are normally held. The modern lacertilian pose when at rest involves a right angular posture of the brachium, with elbow near the ground, and hence with the forearm directed forward. In slow locomotion the manus is advanced partly beneath the body, and the arm is then extended and retracted, with some abduction. Locomotion by primitive reptiles was doubtless much the same, except that the extent of the movements was probably more restricted. In their evolution toward the Mammalia the limbs of the Reptilia underwent certain essential modifications, however. This must have included first a backward rotation of the elbow, so as to bring the manus closer to the midline during all phases of locomotor action, and finally, straightening the arm, so that the animal could stand with the minimum of fatigue. This was almost certainly a vital step in the evolution toward an active, predatory, warm-blooded mammal, and it is one that the reptiles appear to have had the greatest difficulty in encompassing. They did it, however, and the result, in change of posture, has had an important and inevitable effect in the alteration of the angle of leverage of a number of muscles. This, in turn, has accomplished modification in muscle units and in the shape of the parts of the skeleton to which they are attached.

SKELETON

The cleithrum was present only in some members of the Cotylosauria particularly, and of the Theromorpha, at times being vestigeal in the latter; but it disappeared as a recognizable entity in Triassic times. Otherwise the clavicle and interclavicle are the only parts of the membranous girdle that survive in reptiles. The former is usually present, but is lacking in Crocodilia, Ophidia, mosasaurs and some saurians, while it is absent or vestigeal in Pterosauria and Dinosauria (Williston). The interclavicle, on the whole, may be said to be at first most often

spatulate and long. Later it frequently became T-shaped and shortened, disappearing in Pterosauria, Dinosauria, chameleons, and some Plesiosauria (Williston).

It is impossible to state that *all* Permian reptiles had a suture dividing the scapular from the coracoid area, for in a few forms this is not apparent, and in some cases it disappears with advancing age. Nevertheless such a suture is characteristic of the reptiles. Most of the early forms also had a suture marking off the coracoid into two areas. This is the rule in the Cotylosauria, although it too may disappear in aged individuals. With rare exceptions among pelycosaurs this statement also applies to Theromorpha. In the Lower Permian *Varanosaurus* the part of the coracoid posterior to the suture is relatively minute, while in the related *Varanoops* this was either lost entirely or remained permanently unossified (Williston). In *Ophiacodon* its ossification was much delayed, thus suggesting a reduction (Romer). Archosaurs (thecodonts, crocodiles, dinosaurs) on the whole had girdles that were quite narrow, with the coracoid undivided by suture, and this is the case in chelonians (the "procoracoid" in that group is a proscapular process). In living, lizard-like reptiles the coracoid is also undivided by a suture, but in many the surfaces are broad and the entire bony complex, including scapula, comprises in adults a single plate.

The identification of the single coracoid component in later reptiles and interpretation of the condition in mammals have involved one of the most controversial questions in morphology. To review the evidence that has been presented would require a volume, but a brief indication of the points at issue is in order.

The chief effort in the consideration of the problem of the coracoid has usually been directed toward an attempt to identify the coracoid divisions in modern reptiles and birds, monotremes, and placental mammals, but the basic arrangement in primitive reptiles is also in dispute. Of the earlier discussions it is not necessary here to speak. Some of them were excellent for the period but the consideration of evidence subsequently discovered renders obsolete many of the arguments advanced. Hence, only the more recent work will be briefly summarized. Unfortunately, individual investigators have attached such various interpretations to the terms in common use that there is much confusion now attached to them. I shall therefore, for the sake of conciseness, refer in this spot only to the three possible components of the coracoid under discussion as coracoid 1 anteriorly (for the epicoracoid), coracoid 2, and coracoid 3 posteriorly.

According to Gregory, and Hanson, in considering representation in primitive reptiles, modern reptiles, monotremes, marsupials, and placentals, coracoid 1 occurs in monotremes and fetal marsupials, coracoid 2 in all, and coracoid 3 (as well as the other two) only in primitive reptiles (but possibly vestigeal in some others). This school of thought thus believes that the coracoid of modern reptiles and placentals, and the posterior division of monotremes, are homologous. Gregory was first inclined toward this belief by the discovery that in *Moschops* there was evidently a cartilaginous element anterior to the two osseous coracoids, thus suggesting that the latter completed a trio of coracoids. Accordingly he considered that fundamentally there is (a) an epicoracoid (*Sphenodon*, lizards, monotremes) dorsal to the clavicles which never reaches the glenoid; (b) the element usually termed procoracoid but which Gregory considered the coracoid, posterior to the clavicle, pierced by

the coracoid foramen, and contributing to the glenoid; and (c) a metacoracoid, contributing in early reptiles to the posterior glenoid, but lost in modern reptiles and mammals except as it may occur as a vestige. Thus Gregory considered that the posterior division of early reptiles is not found in living vertebrates. He was led to this belief largely because of the degeneracy of the posterior division (metacoracoid) in *Varanosaurus* and *Ophiacodon*, and by the position of the individual divisions in respect to the glenoid.

Gregory (correspondence) has now modified his belief as expressed above—as one is constantly compelled to do in morphology—to the extent that he considers that coracoid 3 (metacoracoid) has not been lost by modern reptiles, but is represented in an undivided condition.

As opposed to this opinion of Gregory, and Hanson, it has been considered by Broom, Watson, and Romer, that coracoid 1 (epicoracoid) constitutes merely a cartilaginous margin of coracoid 2; thus that basically there are only two coracoids. They claimed that where but one representative is found it is the more cranial (coracoid 2) in modern reptiles, the more caudal (coracoid 3) in placentals (and adult marsupials), while both occur together in primitive reptiles and monotremes (and fetal marsupials). They thus believed that the single coracoid of modern reptiles is not homologous to that of placentals.

It is firmly believed that no permanent solution of the coracoid problem can be attained by using the methods heretofore followed, for there is much excellent evidence in support of both theses. An approach from another morphological angle appears to hold more promise, and some explanation of the basis for the arguments employed will be necessary.

One is prone to follow common usage, without particular analysis, in his methods of approach to a problem. In tetrapods common usage has accustomed us to group the elements by segments, as of the brachium or carpus, although in the piscine stage all bones of the appendage were basically of the same value. The humerus is a definite entity, and we do not look upon various sutures as marking off from the humerus separable elements. We term them processes of the humerus; but they are more than mere bony prominences and their definition depends upon muscular stimuli. We think of the greater tuberosity as the prominence of the supraspinatus, infraspinatus, and teres minor muscles. In the whalebone whales the prominence of the "greater tuberosity" is determined by the deltoid muscle, however, and I think all will agree that it therefore merits a distinguishing term, for it is not the same detail as the usual greater tuberosity.

The cartilaginous girdle is just such another case as the humerus. The shoulder *element*, corresponding to the brachial element, is, however, the paraglenoid ossification. This, like the humerus, can develop processes which may become marked off by sutures, but they are extensions of the paraglenoid and not separate elements. The segment has been much affected, in what manner one cannot be sure, by the contiguous membranous girdle, with which it fuses, but at least comparative anatomy indicates that the growth from the paraglenoid region has been in three directions—dorsally, cranially, and ventrally. In such an animal as *Eryops* this consists of an expanse of bone without sutures, which is generally known as the scapulocoracoid. This is a justifiable term, the "scapula" being the part of the area giving rise to dorsal muscles, and the "coracoid" to ventral or flexor muscles. In Lower Permian cotylo-

saurs these two areas of the paraglenoid came to be marked off from one another by a suture, which passed through the glenoid. We know exactly which areas lie on either side of this suture, and that its absence does not indicate the disappearance of either scapula or coracoid areas. Similarly with the ventral division. The coracoid part of the girdle may in turn have a suture marking it off into two areas, and the position of this suture can vary.

As already indicated, we know little of the reason for sutures. Presumably they indicate separate centers of ossification, and the more distinct they are the more advanced the age, by and large, at which they disappear. Presumably also they are associated with areas of muscle stress, as well as other obscure things. Usually they mark areas of distinct muscle groups, although a division of one muscle group can easily invade the territory of a neighbor. Where a small area, as an epiphysis, is separated by suture it usually indicates a purely local stress, as the attachment of a single strong tendon. But one cannot say why sutures are present in some instances and are absent in others. At least it is certain that the absence of a suture does *not* mean that a part of the girdle is absent, but merely that it is undefined by suture.

The reason why the borders of some broad bones remain cartilaginous is also obscure. Such cartilages are prone to develop where there is attachment to other elements, as upon the sternal border of the coracoid. The muscles attached to them are almost invariably very broad ones. They might well indicate disappearing elements, but seldom can be interpreted in this light. It seems that the only safe course to follow is to call them, in the present case, the unossified portion of the dorsal, cranial and ventral borders of the girdle, their extent contracting or expanding locally as different stimuli are encountered. In such diverse forms as *Heloderma* and *Uroplatus* cartilage remains only upon the dorsal and ventral borders, disappearing between, but in *Iguana* the cartilage is continuous upon three sides, narrow upon the sternal border of the coracoid and enormously expanded dorsally to form the suprascapula. With age the latter calcifies completely, while calcification of the remaining part is complete only here and there.

In old individuals of *Iguana* the ossified part of the girdle occurs as a single plate, without sutures. It is expanded in supraglenoid, preglenoid, and infraglenoid directions, the latter having a pronounced posterior process which extends caudal to the level of the glenoid. Directly cranial to the glenoid is the coracoid foramen. Distinctive features are the four fenestrae, bounded on three sides by bone and on the fourth by cartilage. The number of fenestrae may be significant, but not their mere occurrence. They are covered by membrane, from which muscle fibers may arise. Their occurrence is probably possible only where the localized muscle stress is not strong.

Clavicles are well developed in *Iguana*, attached dorsally to the anterior part of the suprascapula where this adjoins the scapula, and ventrally to the interclavicle. The latter is T-shaped, with processes diverging midway between clavicle and the body of the interclavicle. This is situated between the two halves of the girdle anteriorly, and between the two halves of the sternum posteriorly.

When we come to examine the skeleton of a subadult *Iguana* it is seen that the girdle does have a suture, running from the glenoid to the lower border of the second fenestration. Above the line of this suture, then, is the scapula and supra-

scapula, and virtually all of the two upper fenestrations, while below lies the coracoid portion of the girdle surrounding the two lower fenestrations. Let us examine the muscular significance of these facts.

It is clear that in modern reptiles the suprascapula is the skeletal division concerned with the suprazonal muscle group, for all of these muscles insert upon it and nowhere else. Hence it is permissible to assume that in *Iguana* the great development of the suprascapula is correlated with the exigencies of these muscles. It has an additional stimulus, however, for the disappearance of the cleithrum has allowed m. dorsalis scapulae to settle upon the suprascapula. Presumably the latter muscle has increased its function, inasmuch as it has encroached upon the clavicle also. It covers the dorsal fenestration of the scapula.

The chief function of the scapula is probably as a brace for the suprascapula and clavicle. It now constitutes in reptiles the girdle division concerned with those axillary muscles which have left the membranous girdle. These comprise mm. subscapularis and scapulohumeralis, the latter arising partly from the anterior cartilage of the scapula. The remaining axillary muscle, the deltoid, still arises from the clavicle, as originally. Where there is no clavicle, as in Caudata, the deltoid has settled upon the girdle and may build out a considerable process, erroneously termed procoracoid process. This, in reality, is the homologue of the acromial process of Salientia, as suggested by Anthony and Vallois, with which the deltoid has become associated after having left the clavicle, and appears to have its counterpart in the Chelonia, although I have not analyzed conditions in that order and cannot be sure. The term procoracoid in this connection is misleading and extremely objectionable, for it is associated with axillary muscles of the same group as those arising from the scapula, and for it should be substituted the name proscapular process. Its only representative in the Mammalia is the acromion. This completes the dorsal or extensor division of the girdle.

The ventral division of the girdle, from which basically flexor muscles alone arise, is the coracoid portion. Concerned

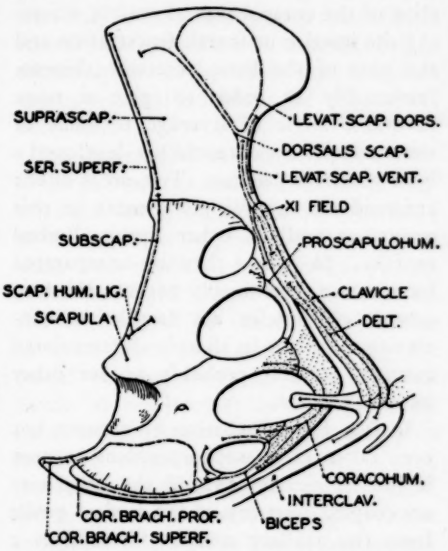

FIG. 1. LATERAL VIEW OF RIGHT SHOULDER GIRDLE OF IGUANA, SHOWING MUSCLE ATTACHMENTS

Clavicle and area of origin of anterior coracoid muscle matrix stippled.

with the coracoid are two distinctive muscle groups, the coracohumeral or supracoracoid matrix, and the coracobrachial matrix. Slips of these can readily be differentiated by their nerve supply. The area of bone from which arises the coracohumeral group may be called the anterior coracoid, and the part giving rise to the coracobrachial group the posterior coracoid. In *Iguana* the muscle concerned with the anterior coracoid is the single

coracohumeralis, which covers the third fenestration of the girdle and has extended ventrally so as to cover a small part of the fourth fenestration. In addition, a few fibers of this matrix have become secondarily fused with the origin of m. coracobrachialis profundus, to this extent encroaching upon the posterior coracoid area (not indicated in fig. 1).

In *Iguana* the posterior coracoid is the area of the girdle from which arise the slips of the coracobrachial matrix, covering the inferior or fourth fenestration and the part of the bone posterior thereto. Presumably in order to give a more favorable angle of leverage to some of these muscles the coracoid has developed a bold posterior process. Two areas of the coracoid are accordingly present in this genus, as well as other living, limbed reptiles. In *Iguana* they are unseparated by a suture, presumably because the two groups of muscles act largely in continuity, and not in sharply differentiated manner, as well probably as for other obscure reasons.

In the above discussion no account has been taken of m. subcoracoideus because it has so clearly invaded the otherwise unoccupied territory of the medial girdle from the axillary matrix. It is thus a dorsal division that has spread over the province of the ventral musculature, just as the ventrally derived suprascapular musculature in mammals has invaded the territory of the dorsal musculature.

It will be noted (fig. 1) that in *Iguana* there is a considerable area of the coracoid from which no muscle arises. This may be considered in this case as a sort of no-mans-land. At least one cannot decide whether it belongs more properly with the anterior or posterior division. If a suture appeared between the two areas it might run in a vertical direction through the fenestra, thus excluding the anterior coracoid from the glenoid, as is the case in monotremes, or it might extend through the inferior fenestration and the glenoid, as in so many primitive reptiles. It is thus considered that the position of the coracoid suture is not of basic importance, but indicates merely the line of stress.

There is every reason for assuming that all primitive tetrapods had the above two groups of flexor muscles; therefore that fundamentally *Eryops* had an anterior and a posterior coracoid division, although these were not separately defined by a suture. When a suture appeared in cotylosaurs this did not alter the essential facts. Similarly when the suture disappeared in modern lacertilians the two areas were still present just the same. Even in Crocodilia, with narrow coracoid, muscles of the two groups arise from the bone and it represents undivided anterior and posterior coracoid areas. Furthermore, no divisions could be basically added, except as accessory epiphyses. There appears no more reason for recognizing the anterior cartilage of *Moschops* as a separate element of the girdle than the cartilage between coracoid and sternum of *Iguana*. They are both merely cartilaginous portions of the coracoid. There is also no reason to suppose that in such a reptile as *Varanosaurus*, with relatively broad coracoid, the coracobrachial area (i.e. posterior coracoid) was reduced to the size suggested by the posterior epiphysis or cartilage. Such is a possibility, but it is more likely that it marked the origin of the tendon of m. coracobrachialis longus—not of the whole group of muscles, the remainder of which probably extended along the coracoid proper.

It is hence claimed that there are basically four areas of the cartilaginous girdle, comprising suprascapular, scapular, anterior coracoid, and posterior coracoid divisions, in conformity with the four

groups of muscles involved, and that all four were present in Permian and Triassic reptiles, irrespective of the number of sutures present, or whether or not these sutures exclude certain areas from the glenoid. Such variation is attributable to differences in muscle attachments and consequently in stresses. The posterior coracoid area could expand and the anterior contract or vice versa, within certain limits. Furthermore, some alteration in the composition of an area could occur, because of the migration of one of its muscles to an adjoining area, but as long as one of its original muscles remained the area should be considered as present, although to a modified degree. Carrying the argument still further it is claimed that all four girdle divisions are also present in living lizard-like reptiles—that there are anterior and posterior coracoid areas, not merely a single one as generally believed.

It is not possible to make the statement that all reptiles that have ever lived had two coracoid areas. So far as I can judge every tetrapod has had coracobrachial muscles originating from the girdle, so the posterior coracoid is uniformly present. In some extinct forms, however, it appears that the coracohumeral musculature had left the coracoid, and in such case the anterior coracoid area would be lacking. In such reptiles as *Dicynodon* one can be sure that an anterior coracoid area is present, because there is a suture to indicate the fact, but the acromion shows that a part of the coracohumeral musculature left the coracoid on its way to becoming the suprascapular divisions. The situation is not clear in some of the dinosaurs with very small coracoids without sutures. It is indicated that in them none of the coracohumeral musculature migrated to the scapula, but it may all have settled down upon the sternum to act as a pectoral division, and in that case also the anterior coracoid would be lacking.

Many investigators have set great store by the position of the coracoid foramen. Thus Gregory used it in part to identify what he termed the coracoid proper of the ventral plate. Such foramina may exhibit much conservatism, while again they migrate, in accordance with the position of the nerve concerned. The fact that the partial homologue of the coracoid foramen is represented in mammals by the suprascapular notch shows that this is an untrustworthy criterion for identifying bony areas.

It seems to have been the rule in cotylosaurs and pelycosaurs of the Lower Permian for the clavicle to have been fused to the girdle throughout its length, and under this condition no acromial process could well exist. As soon, however, as the ventral end of the clavicle became loosened from the girdle, leaving the dorsal end attached, an acromion was likely to result, just as this is barely indicated in *Iguana*. Hence the acromion marks a restricted articulation of the clavicle with the girdle. In its most primitive form this was located upon the anterior border of the girdle, but in two groups of theromorphs at least—Upper Permian and Triassic dicynodonts particularly, and to a lesser extent in Triassic theriodonts—the acromion has retreated somewhat from the border, resulting in a scapular spine and space anterior thereto which was clearly occupied by a supraspinous muscle. The same course of evolution appears to have been barely initiated by later cotylosaurs, such as *Pariasaurus*.

The glenoid presents a rather graphic record of the changes that have occurred in the fore-limb in its evolution from the typically amphibian to the typically

mammalian scheme. This has been discussed many times, most thoroughly perhaps by Romer, but the present contribution would be incomplete without a résumé of conditions.

Many of the earlier Permian reptiles had a glenoid that was entirely on the lateral surface of the girdle, no part of it being situated upon the posterior border. This is an indication that the humerus was held largely parallel to the ground and essentially at a right angle to the body. The screw-shaped type of glenoid was uniformly present in both cotylosaurs and pelycosaurs, its conformation suggesting that during locomotion the distal end of the humerus must have described an ellipse through an arc of but slightly greater than 20 degrees (Romer). The brachium was thus but little more than a lever for elevating the body, this rotating for the purpose of advancing and retarding the antibrachium. The power of rotation was denied by Watson, but demonstrated by Miner to the extent of some 90 degrees in the case of *Eryops*. Rotation of the humerus was absolutely essential for the type of locomotion concerned. There is apparent in the Middle Permian a tendency for the glenoid to shift to the posterior border of the girdle, but still it pointed backward, rather than downward, and the screw-shape of articular surface is retained. The humerus must still have been held mostly parallel to the body and its degree of movement yet restricted, but at least a start had been made toward securing vertical support and getting the manus beneath the body.

In the African series of Theromorpha (dinocephalians, dicynodonts, theriodonts) the screw-shaped character of the glenoid was lost, suggesting greater latitude in the movements of the humerus, while there developed a change in the direction in which the glenoid pointed, from backward to downward, the latter well illustrated by *Cynognathus*. In the latter the limb must have been held essentially in the mammalian position.

Changes in the shape of the coracoid accompany alteration in the inclination of the glenoid. With a glenoid on the lateral surface of the girdle an extension of the coracoid posteriorly rendered coracobrachial muscles particularly effective in retracting and flexing the brachium. This was also the case, with slight alteration in function, with a horizontal humerus pointing mostly caudally. But with a brachium held more vertically a posterior extension of the coracoid became useless and was reduced.

The humerus in the most primitive reptiles, just as in the Rhachitomi, was tetrahedral. The plane of the proximal portion was tilted from the horizontal so that the anterior part was slightly depressed. The broad surfaces of this part therefore were directed mostly dorsally and ventrally. The anterior part constituted a bold flexor, or really a protractor, process, with sundry smaller protuberances. The distal part of the humerus was also broadened, but its plane was at a right angle to the plane of the proximal portion. Its chief definition was ventrally, in the form of an even more robust flexor process. The terminations of these broad planes of bone were for the purpose of giving increased leverage to the muscles concerned; this arrangement was necessary in mammals of considerable weight employing an essentially squatting type of locomotion.

It seems clear, from the study of muscle groups and their units, that basically concerned with the cranial or protractor process of the humerus was the insertion of m. pectoralis, and not improbably that of the coracohumeral musculature as well, although this may originally have been

grouped more with the coracobrachial matrix. The latter was identified with the ventral expanse of the proximal humerus, while the axillary complex was associated with the dorsal expanse. The axillary insertion most anteriorly located was that of the superficial sheet—mm. dorsalis scapulae and deltoideus together—and this has come to be largely associated with the protractor process also, while the most posterior division—m. scapulo-

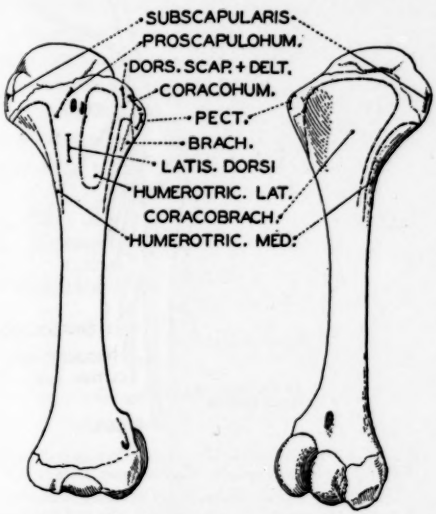

FIG. 2. RIGHT HUMERUS OF IGUANA, SHOWING AREAS OF MUSCLE ATTACHMENTS OF THE PROXIMAL END
Dorsal view on left, ventral view on right

humeralis (later subscapularis)—was concerned with the retractor process posteriorly. It is likely that the first humeral association of m. latissimus dorsi was also with this process, but it probably shifted distally to a more favorable angle of leverage, appearing to have developed a process in the Rhachitomi at least. Later it shifted from one side of the shaft to the other as described in the discussion of this muscle.

At the distal end of the humerus the bold flexor or ventral process was concerned with the origin of the antibrachial flexors, and the dorsal process with the corresponding extensors, more weakly developed. The anterior surface of this distal expanse must have been covered by the brachialis, and the posterior by the triceps.

Except for the facts that the extremities of the bone have been separated by the development of a slender shaft, and that these terminations are much less strongly developed, the humerus of living lizard-like reptiles is very similar to that of their primitive relatives. The flexor process, at each end, is more prominent than the corresponding extensor, as originally. The plane of the distal extremity of the bone does not now lie quite at a right angle to that of the proximal end but at about 45 degrees because of some degree of inward rotation of the arm. The muscle plan, with minor adjustments, still conforms to the basic arrangement described above, except for the difference that the two divisions of the humerotriceps have invaded, on either side of the latissimus, the field of the axillary musculature, as shown in figure 2. Similarly the brachialis origin has moved proximally so that it comes to lie between the coracobrachial insertion and the origin of the humerotriceps lateralis.

NERVES

As in all other tetrapods the brachial plexus of living reptiles is built upon the three trunk plan. In Caudata the brachial axis is almost always through the fourth spinal nerve. Usually the third receives increment also from the second, which may be in the nature of a lag, and occasionally the sixth contributes to the fifth, being an added step in the posterior migration of the plexus. In the Salientia, with their high specializa-

tion and shortening of the spinal cord, there has probably been a secondary retreat cranialward, as well as concentration, of the plexus, so the axis is through the third nerve, with substantial contribution usually only from the fourth.

One may presume that in primitive reptiles also the plexus occupied a position more cranial than in mammals. In certain aberrant living forms, or if one prefer, those with more primitive nervous arrangement, such as *Pseudopus* and *Chamaeleo*, the axis of the plexus has migrated caudally only as far as the fifth spinal nerve (Fürbringer). At the other extreme is *Crocodilus*, with axis through the ninth nerve. Usually, however, this passes in modern reptiles through the seventh or eighth nerve, with a second and third trunk on either side of the central one. An additional root may contribute to either one of these peripheral trunks or to both (more often from above). Thus, there are usually at least four nerves supplying the plexus, occasionally but three as in the chelonian *Trionyx*, and at times five (some geckos and some iguanas). The plexus is supposed to arise from four roots in most lacertilians, but the discovery by me, only after intradural stimulation of the nerve roots, that some individuals, but not others, of *Iguana* receive a fine, very high, contribution also from n. 10, renders uncertain unverified assumptions that the plexus is limited to four roots. In *Iguana*, then, the brachial plexus arises from 4 or 5 spinal nerves, 6 to 9 or 10 inclusive, with axis through n. 8, the contribution from 6 being small, and that from 10, when it occurs, threadlike. In *Iguana* the brachial nerves are readily separable into a dorsal and a ventral group.

As already stated the nerve supply offers entirely dependable criteria for the identification of muscles, with an occasional complication introduced by fasciculation. Thus if a muscle of one matrix comes to function with a second matrix, the nerve supply of that muscle will tend to align itself with the nerves of the second matrix. In other words, within certain limits the nerves of muscles which function together will tend to be grouped together, when no obstacle is encountered.

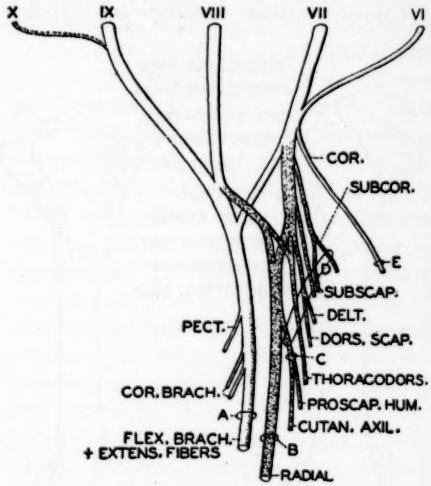

FIG. 3. RIGHT BRACHIAL PLEXUS OF IGUANA: SUPRAZONAL AND INFRAZONAL NERVES NOT INCLUDED

Dorsal division shaded, ventral division unshaded. *A*, passing between mm. coracobrachialis and humerotriceps medialis. *B*, passing between mm. coracoscapulotriceps and humerotriceps medialis. *C*, passing between mm. scapulotriceps and humerotriceps lateralis. *D*, nn. axillares communes. *E*, toracoid foramen.

In many cases nerve pathways are an invaluable aid to the interpretation of muscle homologies, providing that this criterion be used with care. If a slip separate from the surface of a parent muscle its nerve may pierce the muscle (i.e. coracobrachial head of the biceps in *Iguana*). But there is no certain evidence in myology that a muscle nerve ever migrates from one border of a muscle which it does not innervate to the opposite

border by successively piercing the muscle at different points. Where such appears to have been the case it is always some process such as a muscle origin retreating on one side of a nerve and then advancing upon the other side.

A brief discussion of the nerves supplying the shoulder muscles of *Iguana* is presented below. The determination of the derivation of individual branches has been tentatively established in part by the results of electrical stimulation.

N. vago-accessorius. Several fine branches, representing this component, diverge from the vagus and enter the sternocleidomastoideus, whence they are distributed to the remainder of the trapezius sheet. Entering this field are also nn. 3, 4, and 5.

Nn. hypobranchiales. These, to the hypobranchial musculature, are branches from n. hypoglossus, which receives contribution also from sp. nn. 1 and 2.

Dorsal (extensor) division

Suprazonal group

Rami musculares breves from sp. nn. 4 to 9, supplying innervation of the mm. levator scapulae and serrati.

Shoulder group

N. thoracodorsalis. This is considered as separate from the axillary nerves only because it is so distinct in all tetrapods. It appears to be derived from nn. 7 and 8 (9?), and thus is located in the middle of the plexus much as in mammals, instead of upon the posterior border, from the last brachial root, as in Amphibia. This may indicate a shift in the relative position of its motor nucleus; but why this is the case one cannot say. The nerve supplies m. latissimus dorsi.

Nn. axillares communes constitute the remaining branches of the dorsal division supplying the shoulder musculature proper. The following branches may be recognized: 1) *n. dorsalis scapulae* to the muscle of that name, and 2) *n. deltoideus* to the corresponding muscle. Both this and the last are twigs of a single axillary branch that is derived from n. 7, or 6 and 7, and which emerges from between mm. subscapularis and serratus superficialis. N. deltoideus crosses the deep belly of the m. dorsalis scapulae. 3) *N. proscapulohumeralis* appears to be derived from n. 7, 8 (and 9?), and with an axillary cutaneous branch passes beneath the origin of the scapulotriceps to supply the muscle of the corresponding name. 4) *N. subscapularis*, single or double, appears to be derived from n. 7, or 6 and 7, and supplies m. subscapularis. 5) *N. subcoracoideus* to the muscle of this name, occurs either as a branch of n. subscapularis, or as an adjoining, independent branch of the plexus.

Brachio-antibrachial group

N. radialis. The nerve here termed radial follows, on the whole, the course usual in mammals. It passes between the heads of the scapulotriceps and humerotriceps medialis, in the brachium curving around between the two parts of the humerotriceps, which it innervates, and then piercing the ectepicondylar foramen. Additional dorsal fibers to the antibrachium and manus, however, are incorporated in n. medianus, as described in a separate paper. Thus the long extensor nerve fibers of this appendage follow two pathways, as is frequently the case in Amphibia, but with a different arrangement.

Ventral (flexor) division

Infrazonal group

These fine filaments come off the brachial nerves well dorsal to the actual plexus. They supply mm. costoscapularis and the two divisions of sternocoracoideus.

Shoulder group

N. pectoralis is the dorsalmost branch of the common flexor trunk, as is frequent in Amphibia. It innervates m. pectoralis.

N. coracoideus is the most dorsal of the brachial nerves from the anterior cord of the plexus, as in Amphibia. It passes through the coracoid foramen before supplying the coracohumeral musculature and (secondarily) a small part of the coracobrachialis.

Nn. coracobrachiales appear usually to number two. They leave the common flexor nerve next below n. pectoralis, as in Amphibia. They disappear beneath the caudal border of m. coracobrachialis superficialis and innervate the coracobrachial matrix, including the proximal division of m. biceps.

Brachio-antibrachial group

N. flexor brachii. This term might well be qualified, for the nerve also carries dorsal fibers to certain extensor muscles of the distal extremity. It passes between mm. coracobrachialis and humerotriceps medialis—not with n. radialis. In the brachium it gives off twigs to m. brachialis and the distal division of the biceps, before dividing into median and ulnar trunks. It is derived from the four posterior brachial nerves, but electrical stimulation indicates that fibers from n. 10 innervate only the flexors of the wrist and manus.

MUSCLES

The plan of musculature of living reptiles is separated from that of mammals by such an immense interval of time that there are naturally differences. That conditions in one group can be so satisfactorily interpreted in terms of the other is not only gratifying but quite astonishing. The shoulder musculature of *Iguana* may be described as follows:

Branchiomeric division

In this animal the accessory field is divisible into two contiguous portions.

M. trapezius has broad, aponeurotic origin from the dorsum. Insertion is peculiar in that the posterior portion is attached for several millimeters by fasciculi to the middle part of the anterior border of the suprascapula; while the more anterior part of the muscle inserts upon a ligamentous band attached at one end to the dorsal boundary of the insertion of the posterior portion of the muscle, and ventrally to the dorsal part of the clavicle, bridging the area between (fig. 4, C).

M. sternocleidomastoideus adjoins the last but is clearly separable. It is a much thicker division than the trapezius, originating by superficial aponeurosis from the posterior cranium, and by muscle fibers from the posterior border of the skull. Insertion is partly divisible, deeper fibers inserting upon the clavicle and more superficial ones upon the lateral process of the interclavicle.

In *Uromastix* conditions are essentially similar; this may be said of the insertions in *Sphenodon* but its trapezius is much less extensive; in *Cyclura* there is poor separation of the two divisions.

Innervation of the complex in lacertilians is by the spinal accessory nerve, and in addition several cervical nerves enter the muscle. In *Iguana* these are nn. 3, 4, and 5 (4, 5, and 6 in *Sphenodon*).

It may prove tempting to consider the trapezius as representing a dorsal branchial constrictor and the sternocleidomastoid as a ventral constrictor. On the one hand there is no evidence in support of this thesis, and on the other Fürbringer (1900) has demonstrated that in recent lacertilians there are all stages encountered, from a simple undivided condition

of the accessory field to one in which the sternocleidomastoid is completely separable. Hence it appears that the latter is a derivative of a trapezius sheet.

In Amphibia spinal nerves to the trapezius have not been detected, but they occur in amniotes. In *Iguana* sensory fibers must follow this pathway. In some individuals, and in the alligator, no motor fibers could be found, by electrical stimulation, to reach the vago-accessory field via a spinal pathway, but in a particularly large individual motor fibers were found in nn. 3 and 4, but not in 5. Hence, in this respect reptiles doubtless are as variable as, if not more so than, are mammals.

Hypobranchial division

As explained in a previous part of the present study it is felt that no attempt should be made to homologize precisely the hypobranchial units of lower vertebrates with those of mammals. The same treatment will be adopted in the case of reptiles, admitting that such conservatism may not be justified, for the three divisions in *Iguana* show considerable similarity to the three divisions in mammals.

In *Iguana* the more dorsal division arises from the anterior border of the ventral half of the suprascapula and dorsal half of the clavicle, and inserts upon the lateral half of the hyoid. The middle division arises from the lateral process of the interclavicle and inserts upon the medial part of the hyoid and anterior part of the first (third) branchial cartilage, which in this form follows the midventral line. The third hypobranchial division arises from the anterior part of the interclavicle and inserts upon the dorsal surface of the anterior part of the first branchial cartilage. In *Sphenodon* there are but two divisions of this complex, one arising from the border of the scapula and the other from both clavicle and interclavicle.

Innervation, reputedly by cr. n. XII, and sp. n. 1; not sought by me.

Dorsal (extensor) division

Suprazonal (or serratus) matrix

M. levator scapulae occurs in two divisions. Both arise apparently from the transverse process of the atlas only. The more superficial and larger pars dorsalis then diverges to insert upon the middle (not the anterior) third of the suprascapula, the posterior line of insertion being oblique and adjoining the origin of the dorsalis scapulae. The pars ventralis lies partially deep to the other division and inserts upon the ventral portion of the anterior border of the suprascapula.

Iguana is apparently representative of the lacertilian condition of the levator scapulae, while in *Sphenodon* the insertions of the two divisions are farther apart; these thus illustrate two of the stages in the separation of this muscle mass that culminates in certain mammals. In some reptiles (*Sphenodon*) origin is from the axis as well as atlas.

Innervation: Nn. 4, 5, and 6.

Mm. serrati. The complicated arrangement of the serrati in lizards has been exhaustively discussed several times and as they are of little importance to the present study a detailed description is not advisable. The slips occur in three groups: a) a posterior sheet, usually termed superficialis, extending ventrocaudally from the posterior border of the suprascapula to two ribs; b) a sheet two segments wide immediately beneath the suprascapula with fibers parallel to those of a); and c) a broader, deeper sheet covering four or five segments, with fibers inclined cranioventrally, and hence almost parallel to those of the levator

scapulae. Innervation is by the adjacent spinal nerves.

Undoubtedly the levator scapulae and serratus divisions have been differentiated from a single complex. The former advances and depresses the suprascapula and is assisted by the deepest sheet of the serratus. The superficial serratus depresses and retracts the suprascapula and is assisted by the more superficial sheet of the deep serratus. In mammals the levator scapulae part remains distinct, and it is likely that the serratus divisions have experienced realignment so as to

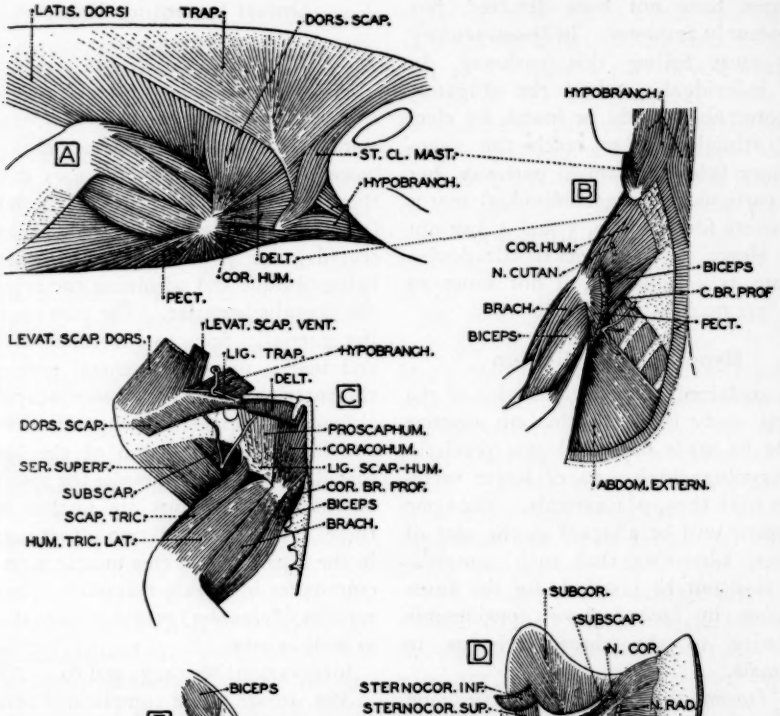

FIG. 4. MUSCULATURE OF THE RIGHT SHOULDER REGION OF INGUANA

A, superficial details in lateral view. *B*, ventral aspect, with pectoralis cut. *C*, lateral view of deeper details; vago-accessory field, part of hypobranchial musculature, and insertions of dorsalis scapulae, deltoideus, and pectoralis removed. *D*, medial view of shoulder. *E*, lateral view of brachial flexors; overlying muscles removed.

operate on a more mobile scapula in a single sheet. Romer (1922) is of the opinion, however, that the reptilian serratus superficialis is not represented in mammals.

A rhomboid division has not been developed in modern reptiles except by the Crocodilia.

Shoulder group

Thoracodorsal (latissimus) matrix

M. latissimus dorsi has broad origin in *Iguana*, extending anteriorly so as to cover a part of the dorsalis scapulae. It converges to a tendinous insertion upon the more dorsal part of the protractor (flexor) process of the humeral head. Conditions are similar in *Sphenodon*. Innervation: N. thoracodorsalis (from nn. 7, 8, and 9?).

The interesting point in regard to the latissimus is the manner in which its insertion has migrated. In *Necturus* its pull is in the same plane as the triceps group. Hence it is an extensor of the upper arm, without rotational action. In *Rana* the insertion has shifted to one extreme, over the lateral surface of the humerus to the flexor tuberosity. Hence the muscle not only has a longer pull, but is a lateral rotator as well as a retractor of the arm. This is doubtless correlated with the extreme akimbo position in which the anuran arm is held. In *Iguana* the latissimus insertion has shifted toward the opposite extreme, having migrated medially to an association with the brachial flexors; so that in lacertilians it is not only a retractor but a powerful inward rotator of the arm. This action helps in the fact that in this group flexion of the arm is not straight back, but is accompanied by abduction of the elbow. This shift in the attachment of the latissimus insertion is further explained in connection with m. triceps.

It may here be mentioned that derivation of the mammalian m. teres major is probably from the latissimus sheet, as believed by Romer (1922).

Axillary matrix

This includes those muscles of the dorsal division which arise from the girdle and insert upon the humerus.

M. dorsalis scapulae has origin along an oblique line, adjoining that of m. levator scapulae, which extends from a point near the dorsocaudal part of the suprascapula toward the clavicle. Here origin is both from the dorsal part of the clavicle and from the dorsal margin of the first fenestration of the girdle. A part of the origin is covered by the latissimus (beneath trapezius in fig. 4 A). At insertion the fibers fuse with those of the deltoid and attachment is narrowly upon the lateral part of the protractor process of the humeral head.

Conditions are essentially the same in *Cyclura* and *Sphenodon* except that in the latter origin is more dorsal, rather than oblique. This detail in *Necturus* is also much the same.

Innervation: A branch of the axillary nerve which enters the muscle along its posterior margin.

It seems evident that in basic forms, such as stegocephalians, this was *the* girdle muscle of the cleithrum, just as the deltoid is *the* girdle muscle of the clavicle, and that the two were not only contiguous, but that to all intents the sheet comprised a single muscle. As the cleithrum disappeared the dorsalis scapulae component settled upon the suprascapula and became separated to various degrees from the deltoid. There is no reason for presuming, as do Romer and others, that the two divisions ever fused again to constitute the mammalian deltoid. On the contrary there is every

reason for believing, and none for doubting, that the dorsalis scapulae later became the teres minor.

M. deltoideus (proscapulohumeralis part) is not attached to the cartilaginous girdle at any point but has origin from the inner margin of the ventral two-thirds of the clavicle and inner surface of the anterior interclavicle. Its fibers fuse at insertion with those of m. dorsalis scapulae, and attachment is upon the lateral part of the protractor process of the humeral head. In *Sphenodon* conditions are similar except that origin is purported to be from the lateral aspect of the clavicle (Miner).

Innervation: A branch of the axillary nerve, from nn. 6 and 7, from which also diverges the twig to the dorsalis scapulae. Beneath the latter muscle it passes to the cranial part of the deltoid.

There appears to be but little doubt that m. deltoideus was basically clavicular in origin. Where the clavicle disappeared the muscle settled upon the cranioventral part of the scapula, becoming a scapulohumeralis longus, as in Caudata. A tendency which it exhibits throughout phylogeny is a dorsal migration of its origin. In claviculate Salientia dissociation of the deltoid origin from the clavicle is practically complete, origin being from the girdle dorsal to that bone. In lacertilians it is still entirely from that bone, and hence has nothing to do with the cartilaginous girdle.

M. proscapulohumeralis (procoracohumeralis brevis, scapulohumeralis anterior). At origin, which is from the lateral surface of the girdle around the anterior margin of the second fenestration, this muscle immediately adjoins m. coracohumeralis and is in the same layer. Toward insertion, however, the latter muscle passes over the ligamentum scapulohumerale while m. proscapulohumeralis passes beneath the ligament to insert upon the humerus between the lateral and medial heads of the humerotriceps. Conditions appear to be the same in other lizards considered. Innervation: By a branch of n. axillaris, passing deep to the origin of the scapulotriceps.

The mm. deltoideus and proscapulohumeralis are separated by the tough fascial extension of the ligamentum scapulohumerale, and if such separation were fundamental it would constitute evidence for considering the two muscles to have had separate derivation. The ligament has probably been secondarily developed, however, and it is believed that the proscapulohumeralis of *Iguana* is homologous to the shorter division of the same name in *Necturus*, and that it represents a deeper division of the original dorsalis scapulae—deltoideus layer.

M. subscapularis (scapulohumeralis brevis or posterior) arises from the base of the medial side of the suprascapula and adjoining part of the scapula, and from the caudal border of the latter, barely encroaching upon the lateral surface. The fibers converge to tendinous insertion upon the retractor process of the humerus. The function is inward rotation with slight retraction of the arm. Innervation: By an axillary branch that pierces the medial surface of the muscle.

It is considered that this muscle is homologous to the scapulohumeralis brevis (termed subscapularis in *Megalobatrachus* by Miner) of amphibians, which in reptiles has invaded and spread over the medial surface of the scapula. In *Iguana* and *Cyclura* it is indivisible, but in *Sphenodon* a scapulohumeral slip is distinct from the remainder of the subscapular portion. This separation is probably secondary.

M. subcoracoideus adjoins the subscapularis but is separated therefrom by the scapular attachment of the sternoscapular

ligament and by n. coracoideus. It is largely multipennate in form and arises from the entire medial surface of the coracoid, passes deep (lateral) to the sternoscapular ligament, and inserts upon the capsule of the shoulder joint continuous with the tendon of the subscapularis. It must act as a retractor of the arm. Innervation is either by a twig from one of the branches to m. subscapularis, or by a separate branch leaving the plexus close to n. subscapularis. This frequently follows n. coracoideus for a short distance.

The most logical explanation of the derivation of this muscle is that initiating fibers first diverged from the subscapularis near insertion, and then spread over the medial surface of the coracoid between the bone and the sternoscapular fascia (ligament). The innervation lends strong support to this thesis. Certainly it is a muscle of the dorsal division and there is no other logical source from which it could have come.

Gregory and Camp consider that this slip is represented in mammals by m. coracobrachialis brevis, an entirely unjustifiable conclusion. I subscribe to the opinions of Romer and Miner that the muscle must have been undeveloped, or at least purely vestigial, in early reptiles and mammal-like reptiles, and unrepresented in mammals, because the conformation of the girdle in the first renders it almost impossible that such a muscle could have been effective, as would certainly be the case as soon as the humerus had begun to be held in the typical mammalian position. It therefore follows that the muscle was differentiated only in forms in which the humerus was held in an essentially retarded position and largely parallel with the ground.

Ligamentum axillaris. This is a complex structure an adequate description of which I have not encountered in the literature, but which may be of much importance. It may be considered to consist of two connected portions, termed scapulohumeral and sternoscapular ligaments. The scapulohumeral ligament is largely triangular in form, the dorsal angle being attached to a slightly defined process on the lateral scapular margin just above the glenoid, the ventral angle to the lateroventral process of the humeral head, while the posterior angle of the ligament provides origin for the scapulotriceps fibers. The anterior border of this ligament continues cranially as a tough, aponeurotic fascia, between mm. deltoideus and proscapulohumeralis. The part that forms the tendon of the scapulotriceps extends in a loop distally around the insertion of the latissimus and then continues proximally as the tendon of the coracotriceps, passing to the medial aspect of the girdle. Proximal to the axillary border of the coracoid this tendon spreads out to form the sheet termed sternoscapular ligament. It has a three-point anchorage; 1) broadly along the coracoid border of the sternum and thence continuously to 2) the medial border of the coracoid, and narrowly to 3) the medial surface of the scapula. Upon the mediodorsal surface insert the fibers of the costoscapularis, ventral to it is situated m. subcoracoideus, and covering a part of its dorsal surface is m. sternocoracoideus. In addition, from the medial border of the proximal part of the coracotriceps tendon diverges a tough sheet of fascia which is attached to the humerus deep to the insertion of the coracobrachialis. Thus in *Iguana* the scapulo- and coracotriceps arise from a continuous, tendinous sling or loop, suspended laterally between scapula and humerus, and medially between sternum, coracoid, and scapula. This is a very striking and strongly developed arrangement which may shed

considerable light upon the derivation of triceps divisions.

In *Cyclura* this arrangement is less strongly defined but on the whole is similar, except that the scapulotriceps arises more from the scapula and not so definitely from the stout scapulohumeral ligament. In *Sphenodon* m. scapulotriceps appears to be intermediate between conditions in *Iguana* and *Cyclura*, but descriptions of *Sphenodon* do not stress nor clearly indicate continuity between the tendons of the scapulo- and coracotriceps.

Ligaments are derived from connective tissue and not from bone; hence the sternoscapular ligament hardly is a remnant of the primitive supraglenoid buttress, as argued by Miner, but very possibly of the fascia that was concerned therewith. If derivation of these ligamentous sheets had been purely from capsular ligaments they would occur deep to all the muscles; but they are situated superficial to certain muscles; hence it seems clear that they have developed from fascia. This is further discussed in relation to the triceps.

Brachio-antibrachial group

It is convenient to recognize by name four divisions of the anconeus or "triceps" complex in *Iguana* as follows:

Mm. scapulotriceps et coracotriceps. These are virtually inseparable but it is convenient to differentiate the fibers concerned with the two sides of the girdle. Those considered scapulotriceps arise from the scapulohumeral ligament and from the continuation thereof which loops around the insertion of the latissimus. From the medial part of this tendinous loop arise the fibers of the coracotriceps, the ligament therefrom continuing proximally as a round tendon with attachment to the sternoscapular ligament (fig. 4 C). Common insertion is upon the olecranon.

M. humerotriceps lateralis, between nn. scapulotriceps and brachialis, arises from the caudolateral part of the humeral head and adjacent part of the shaft. Insertion is upon the olecranon.

M. humerotriceps medialis, located between the flexor brachii and extensor brachii, takes origin from the medial head of the humerus just caudal to the insertion of the subscapularis, and from practically the entire length of the shaft of this bone. Insertion is upon the olecranon.

Innervation: Branches of the common extensor nerve or n. radialis.

The same difficulty in interpreting the phylogeny of the brachial flexors is encountered in the extensors of this segment. Because of conditions in *Necturus* it is considered possible that its dorsitriceps (representing a scapulotriceps) may have been derived from the latissimus, aberrant slips having extended down the arm via a fascial route. Even if this was actually the case, however, mergence with the rest of the triceps is so far advanced that one can be certain of nothing: and the situation is, of course, still more obscured in reptiles. With this possible exception, however, I am unable to escape the belief that the triceps has been derived from a brachio-antibrachial matrix, originally having nothing to do with the shoulder. Whatever the primitive origin of the "scapulotriceps" the diversification of its subsequent development indicates that it was not originally connected with the girdle, but that it has experienced during its phylogeny an essentially constant stimulus for reaching the scapula. Or let us express it that there has been a stimulus for some part of the triceps to reach the scapula. In *Rana* origin shifted so as to pass medial to both the latissimus and dorsalis scapulae and eventually reach the scapula; and the fact that it bridges

n. pectoralis indicates that its route was fascial rather than via bone and joint capsule. Furthermore, the fact that in *Rana* it did not encounter the obstacle of the tendon of the latissimus renders it likely that in function, and probably in fact, this head in the frog represents both scapular and coracoid triceps. In *Iguana* it has attained the same functional goal, but by another pathway, which carries it lateral to the latissimus tendon. In this case also the pathway has probably not involved a bony attachment, but migration along a fascial plane, which carried it superficial to the insertion of m. proscapulohumeralis with the arrangement already described. It is only thus that differences in the muscle can be explained.

There is considerable question whether the coracotriceps of *Necturus* is homologous to the corresponding slip in reptiles. Its origin, from flexorward of the brachial nerves, introduces some uncertainty, and the fact that Miner found the proximal part innervated by a twig of n. coracobrachialis in *Megalobatrachus*, which is not the case in *Necturus*, suggests a dual origin. Romer considered that there was no coracotriceps in primitive reptiles, and the division is absent in mammals. In *Rana* an indivisible scapulotriceps subserves the function of both, but in lizards the latissimus tendon intervenes as an obstacle, and this has been overcome by the development of two origins, from scapula and coracoid respectively, for an otherwise indivisible, long triceps. It appears that even in these the coracotriceps part is in course of reduction. Further argument along this course suggests that one would not expect to encounter a coracotriceps separated from a scapulotriceps unless the latissimus tendon is so situated as to require straddling by the long triceps division.

The humerotriceps divisions have shifted around to some extent, and there are indications that there have been recession and advance of their origins. Thus the lateralis in *Rana* has advanced in a proximal direction lateral to the tendon of the latissimus, while in *Iguana* this advance has been medial to the tendon. In *Necturus* the proximal advance of the medial head has been posterior to both flexor and extensor nerves of the brachium, while in *Rana* this head separates the respective nerves, as is also the case in *Iguana*. It is probable that a fairly safe criterion for differentiation of the two heads of the humerotriceps is the course of the radial nerve, which passes between them.

In *Sphenodon* there is an additional brachial extensor — humeroradialis — which is absent in other lizards but which is purported to have a partial homologue in Crocodilia (Fürbringer). It arises from a distal continuation of the ventral part of the scapulohumeral ligament, and inserts partly upon the supinator longus of the forearm. As it is proximally innervated by a twig of the deltoid branch and distally by n. radialis lateralis, it is probably compounded of deltoid and supinator elements (Miner).

Ventral (flexor) division

Infrazonal matrix

There is no certainty that this group should not be accorded a separate division, like the hypobranchial matrix, but it can be included provisionally with the ventral division of the girdle musculature. In *Iguana* it is differentiated into three slips as follows:

M. costoscapularis (costosternocoracoid eus) is the most lateral, arising narrowly from the first sternocostal and inserting upon the dorsal surface of the more lateral part of the sternoscapular ligament.

M. sternocoracoideus superior (sternocor. profundus) is the broadest of the group, arising from the dorsal surface of most of the sternum, and inserting by a broad, thin tendon upon the caudomedial part of the coracoid, on a line parallel with the fibers of the subcoracoideus, muscle fibers of the latter passing upon both sides of the line of insertion.

M. sternocoracoideus inferior (sternocor. superficialis) is much smaller and entirely hidden by the superior division. Origin is from the medial part of the anterior border of the sternum, between the sternoscapular ligament ventrally and the fascia or ligament of the sternocoracoid articulation. It inserts with the superior division.

Innervation: By high, slender filaments from all three brachial trunks, most of that from the first supplying the costoscapularis.

The first two of these muscles are rather uniform in lizard-like reptiles, while the group appears to be represented in all living members of the order (except those without girdles). The third is more variable. In *Sphenodon* origin is more extensive, from not only the entire cranial border of the sternum but also from the first sternocostal. Occasionally it appears to be absent (*Uromastix*).

Miner looks upon this group as a remnant of the sternohyoid musculature, and hence as an anterior representative of the rectus abdominis. This I consider a more precise commitment than the evidence warrants. It appears much better to regard the group merely as ventral slips of the trunk musculature originally passing from the body to the membranous girdle, entirely comparable to the more dorsal serratus matrix.

This group is absent in Amphibia but there is no reason for doubting that it was present in ancient reptiles and in the mammalian ancestry. Its mammalian representative is rather uniformly considered to be m. subclavius, to which hypothesis there appears to be no objection; but no attempt should be made to homologize the latter muscle with any one of the slips occurring in living reptiles.

Shoulder group

Pectoral matrix

M. pectoralis arises from the full length of the interclavicle and from the border of the diverging "xiphisternum," as well as for some distance from the last complete rib. The fibers converge to a narrow insertion upon the ventral process of the proximal humerus. The muscle is partly divisible into a mesocleido-xiphisternal part, and a part originating from the rib. The former is paler colored and the latter more reddish, this difference suggesting some corresponding difference in action. Innervation: N. pectoralis, by way of the axilla, from the posterior part of the plexus.

In *Sphenodon* the posterior part of this muscle has extended beneath the border of the superficial abdominal muscle, rather than superficial to it as seems usual in lacertilians. In *Iguana* it also extends more dorsally than in *Sphenodon*.

If one consider that the pectoralis of *Necturus* illustrates an intermediate condition, in which this sheet covers practically none of the coracohumeralis (supracoracoid) musculature, then modern reptiles represent one direction of pectoral development, with the muscle covering the coracohumeral layer entirely and with extreme anterior extension, while mammals illustrate an opposite trend, in which the coracohumeral layer over-rides the pectoralis, in some forms (man) covering all of the latter muscle.

Mention should here be made of the

mesocleidosternal ligament (fig. 4 B), which is broad and tough, passing from the lateral process of the interclavicle to the anterior border of the sternum, and located just deep to m. pectoralis. Fürbringer (1900) stated that in lacertilians the episternal part of the "sternocleidomastoid" inserts upon this as well as the lateral process, and his figures of *Gecko*, *Zonosaurus*, and *Lygosoma* indicate not only that he considered the relationship of the muscle and ligament very close, but that the latter extends lateral to the process. In *Iguana* this feature did not obtain, but the sternocleidomastoid fibers have nothing to do with the ligament except that a few of them spread over the interclavicular attachment. There is no necessity for considering such ligaments as the remnants of muscles, and it does not seem wise to look upon this one as indicating a former extension of the rectus abdominis. It is really a broadened fascia or ligamentous connection between interclavicle and sternum, and no attempt should be made to make anything more of it.

Anterior coracoid matrix

M. coracohumeralis (supracoracoideus), although not extensive, is a very stout muscle, especially in large individuals. It arises from the anterior margin of the two inferior (third and fourth) fenestrations of the girdle, converging, mostly under cover of mm. deltoideus and pectoralis, to an insertion just proximal to that of the latter muscle. Innervation: N. coracoideus, diverging from the anterior part of the plexus and piercing the coracoid foramen.

The anterior coracoid musculature is secondarily simplified in lacertilians as compared with *Necturus*, and especially *Rana*. Presumably it is also more simple than it was in Lower Permian reptiles. Thus, living reptiles show no initiation of the changes which this matrix experienced in the development of the suprascapular musculature and the pectoralis major of mammals. Dicynodonts and theriodonts, however, and also some of the still older reptiles in lesser degree, indicate by the reduction of the anterior part of the coracoid that a part of the origin of the coracohumeral musculature probably had settled down upon the sternum, thus initiating a pectoralis major component. Similarly, in these forms the conformation of the acromion shows very plainly that a part of this matrix had migrated dorsally, anterior to the acromion, and thus deep to the insertion of the trapezius. This part evidently did not encroach upon the lateral surface of the scapular blade but at first must have been largely confined to the anterior border. Thence fibers could extend posterior to the acromion around its ventral termination, to become an infraspinatus, and medially, to become the anterior part of the subscapularis. That some of the anterior coracoid musculature still originated from the coracoid in these reptiles, however, is indicated by the survival of the anterior division of the ventral part of the girdle.

Posterior coracoid matrix

Four divisions of the coracobrachial group are clearly separable in *Iguana*, and because of their possible importance in later discussion they will be described at some length.

M. coracobrachialis superficialis (coracobrachialis longus). This is divisible into two parts, one (a) with tendinous origin, and the other (b) with fleshy origin. The former arises by a long tendon from the extreme posterior termination of the metacoracoid region of the girdle. Insertion is partly upon the medial epicondyle

of the humerus and partly upon the stout flexor-extensor intermuscular septum of the brachium. Part b) is located superficially between the tendons of part a) and coracotriceps. It has fleshy origin from the medial aspect of the sternal border of the posterior coracoid, passes, like part a), superficial (medial) to n. flexor brachii, and also inserts upon the flexor-extensor intermuscular septum of the brachium. Innervation: Twigs of n. coracobrachialis, and also by another filament diverging from the flexor nerve somewhat below, both passing deep to part b) of the muscle.

This arrangement in *Iguana* appears to be different from the usual condition in lizard-like reptiles, as typified by *Cyclura*, *Uromastix*, and *Sphenodon*, in which the muscle is not readily separable into two parts, and without a definitely tendinous origin. Because of this one may infer that the tendinous head is accessory to the other, possibly having reached its present form by adopting a fascial pathway or appropriating some such structure as the coracoradial tendon of *Megalobatrachus*. Similarity of innervation and of association with the intermuscular septum, as well as situation with respect to the flexor nerve, indicate the unquestionably close relationship of the two divisions.

M. coracobrachialis profundus (coracobrachialis brevis) likewise occurs in two parts, both of which lie deep (lateral) to n. flexor brachii. The more extensive part a) is covered mostly by the biceps, having origin from the lateral surface of the part of the girdle bounded by the posterior process of the coracoid, the glenoid prominence, and the posterior border of the inferior fenestration. Fibers pass, deep to the biceps tendon, to insert upon the proximal half of the medial aspect of the humerus. Part b) is a small slip located between part a) and m. coracobrachialis longus, originating from the tip and adjoining posterior border of the posterior coracoid process, and inserting with the other division, but medial to it. Innervation of part b) is solely by n. coracobrachialis, which passes deep to it. Part a) is innervated chiefly from this source, via its deep belly, but also it indubitably receives a fine filament of n. coracoideus, which enters the lateral border of the muscle near its origin.

Conformation and innervation are the same in *Cyclura*, but in other lizards reported in the literature the muscle appears to be single, and partial innervation by n. coracoideus appears never to have been detected. To my mind this double innervation is interesting as indicating that a part of the coracohumeral (supracoracoid) musculature, probably representing the coracohumeralis minor of *Necturus*, has secondarily become associated with the coracobrachialis profundus, but it is evidently either of transitory significance or else is a development unique in certain lizards, for it appears not to be found in other animals.

Brachio-antibrachial group

The biceps of *Iguana* is a product of both this and the posterior coracoid matrix, but chiefly of the former.

M. biceps brachii is single but occurs as a proximal belly and a distal belly, the two separated by tendon. The former is short, thin, and fan-shaped, arising from the anterior border of the inferior fenestration of the girdle, deep to m. coracohumeralis. Fibers converge to the lateral side of a broad tendon which, deep to the muscle, arises partly from the posterior border of the inferior fenestration and partly from the medial border of the girdle. The tendon passes partly beneath the head of

the humerus and from it arise the muscle fibers of the distal part of the biceps. There is partial fusion distally with the brachialis, but nevertheless insertion of the biceps is essentially upon the ulna. Innervation of the proximal belly is by a branch of n. coracobrachialis, which enters the deep surface after piercing m. coracobrachialis profundus. The distal part of the muscle is supplied by a branch, in close association with that to the brachialis, of n. flexor brachii.

This is the arrangement of the biceps typical of lizards, varying from the condition in which the proximal belly inserts upon the whole width of the tendon (*Gecko*, as well as *Sphenodon*), to that in which the fibers have finally disappeared and the tendon becomes narrow (*Chamaeleo*), as figured by Fürbringer (1900). Conditions in the vertebrates indicate a constant effort to evolve a satisfactory "biceps" out of any material that was ready at hand (*Megalobatrachus*, *Necturus*, *Rana*). In *Necturus* it is not unlikely that the coracobrachial complex was so employed to manufacture m. gleno-antibrachialis. It seems apparent, however, that the lacertilians have either followed a different plan, or less likely that in them a coracobrachial derivation of the distal biceps has been secondarily obscured. At least in their case conditions suggest that the lower division of the biceps became initiated by the divergence of a distal part of the brachialis onto a fascia or intermuscular septum, along which the fibers extended proximally. That this was so is indicated by the association of the nerve to the distal biceps with that to the brachialis. The separate nerve supply to the proximal part of the biceps very clearly shows that that, at least, was derived from a part of m. coracobrachialis which secondarily settled upon the tendon of the biceps. That this proximal part is unrepresented in mammals is highly likely.

M. brachialis originates laterally from the head of the humerus and most of its shaft, between mm. biceps and humerotriceps lateralis. Near insertion there is partial fusion with the biceps, but artificial separation demonstrates that insertion of the brachialis is upon both radius and ulna. Innervation: A branch of n. flexor brachii.

This muscle is considered to be fundamental, constituting a matrix of its own, from which has been derived the part of the biceps brachii which is represented in mammals.

DISCUSSION OF NERVE-MUSCLE ACTION

In the present study the stimulating apparatus used was that described in Part III. Action through motor fibers, by applying current to intact nerves or to the peripheral stumps of nerves that had been cut, was uniformly obtained on animals under ether anesthesia at a threshold not exceeding one quarter volt. Muscular response via particular sensory pathways was secured by applying stronger current, of one half to one volt, to the central stumps of certain nerves that had been transected. It is as yet unknown just what type of sensory fibers carry these electrically excitable impulses—whether they have heretofore been grouped with proprioceptive or some other sort of afferent fibers. Hence, for the present, they will be designated merely by the innocuous term of x-afferent fibers, the "x" indicating the unknown quantity. It is probable that in normal muscle action these fibers constitute the afferent parts of reflex arcs which are brought into play by stimuli supplied by the stretching of muscles, movement of joints, and similar phenomena. In the tests conducted

five specimens of *Iguana* were variously employed in three sets of experiments.

Experiment on the innervation of the accessory field. Five sides of three specimens. The accessory field in *Iguana* is innervated by a group of several fine branches of the vagus, representing a spinal accessory component, and by nn. 3, 4, and 5. The accessory branches enter the extreme anterior border of the muscle sheet, and the spinal nerves farther back. The three spinal nerves were cut. Stimulation of their respective *central* stumps at currents from ½ to 1 volt resulted as follows: Through stump of n. 3, no action of the accessory field, but only a slight tremor of the adjacent trunk musculature; through n. 4, contraction of the sternocleidomastoid only; and through 5, contraction of the trapezius only, particularly the posterior part (not determined in one animal). Stimulation of the *peripheral* stumps was without result in one individual. In a second there was no action through nn. 4 and 5, but n. 3 was damaged and not tried. In a third, particularly large specimen there was strong action of the sternocleidomastoid through n. 3, on both sides; of the trapezius through n. 4 on one side but not on the other; and no determinable action through n. 5.

This experiment indicates that in some cases all the motor fibers to the accessory field of musculature are carried only by N. XI (or its equivalent), while in others a portion of these fibers follow a spinal pathway, those to the sternocleidomastoid being situated more cranially than the ones to the trapezius; that n. 3 carries x-afferent fibers discharging into montoneurons supplying the trunk musculature only; that n. 4 carries similar fibers concerned with the sternocleidomastoid, and n. 5 with the trapezius. A larger series would doubtless show variation from this pattern.

It thus seems that some of the fibers which in anamniotes follow a vago-accessory pathway have, in amniotes, adopted a shorter route. This question is more fully discussed in collaboration with W. L. Straus, Jr. in a paper now in press.

Experiment on brachial plexus: Peripheral approach. The trapezius and serrati were transected and the suprascapula abducted to expose the brachial trunks where these emerge from beneath the dorsal musculature.

Series A. Three sides of two specimens. The three brachial trunks were cut and muscular contraction obtained by stimulating the *peripheral* stumps at low voltage (ca. one-eighth volt). Through trunk 1 there was strong flexion of the antibrachium and moderate flexion of the digits. The brachium was held at a right angle to the body (thus protracted) and two actions were then involved, following separate stimulation of the two borders of the one trunk (evidently because sp. nn. 6 and 7 both contribute to it): a) adduction, and b) slight abduction of the brachium. Through trunk 2 there was rigid extension of the entire limb in a ventral direction. Through trunk 3 there was similar extension of the arm but in a more caudal and lateral position; digits either lax or slightly flexed. In one instance the above action of trunks 2 and 3 showed some reversal. Results otherwise were quite uniform. In another instance the action through trunk 1 could not be repeated subsequent to the application of one-and-a-half volts. Stimulation at one volt of the *central* stumps of the brachial trunks was followed by lateral wriggling of the body.

This experiment indicates that there is the same plan of motor control of the limb as occurs in *Necturus*. The first trunk carries impulses for flexing and protracting the limb beneath the body, the second

initiates extension, and the third completes it, with some intervariation in the action through the two posterior trunks. It should be realized that from this approach the responses are somewhat mixed, for the first brachial trunk carries fibers from sp. nn. 6 and 7, and the third, fibers from 9 and sometimes 10. In *Necturus* there was secured through the third trunk, at a higher threshold, an initiation of recovery toward the flexed position of the limb. This was not observed in *Iguana* during this experiment. At no time was the elbow advanced farther cranially than the level of the glenoid, further protraction doubtless being secured through action of the accessory and hypobranchial fields. The experiment also indicates that action of the limb muscles stimulates, through x-afferent fibers, contraction of the adjacent trunk musculature.

Series B. Both sides of one specimen. On the right side brachial trunks 1 and 3 were sectioned and the central stumps were stimulated. At one-quarter volt there was a tremor toward supination of the wrist. At one-half volt both roots had the same action, violently extending the limb straight back against the body. The same voltage applied to the intact trunk 2 had an identical result. On the left side trunk 2 was cut, leaving trunks 1 and 3 intact. The central root of trunk 2 was stimulated at one-tenth volt without result. As one-half volt there was first contraction of the adjacent trunk musculature, followed after 1 second (circa) by wriggling of the body and movement of all four limbs.

This experiment indicates that x-afferent fibers are carried by trunks 1 and 3; that at least some of these connect centrally with motoneurons whose axons emerge via trunk 2; and that none of the x-afferent fibers possibly carried by trunk 2 are concerned with motor axons emerging by trunks 1 and 3.

Experiment on brachial plexus: Intradural approach. The spinal cord of a lightly etherized *Iguana* was exposed by laminectomy to include what I thought at the time were segments 6 to 10. Autopsy, however, proved that access was thus given to the roots of nn. 7 to 11 inclusive. The dura was slit and reflected. Stimulation at about one-half volt of the intradural part of the dorsal roots of these nerves resulted as follows: Through 7, flexion of forearm with slight protraction of arm; through 8, retraction of extended limb, with action more contralateral than ipsilateral; through 9, retraction with abduction of extended limb; through 10, flexion of wrist only, with moderately extended limb; and through 11, no movement ipsilaterally but indefinite, though quite strong, action by the contralateral member. In all cases there was some vague contralateral, and at times, diagonal limb movement.

The dorsal roots were then cut and the ventral roots stimulated at one-eighth volt, with the following results: Through 7, adduction with slight retraction of brachium, and flexion of antibrachium; through 8, strong retraction of extended arm; through 9, strong retraction, with some abduction, of extended arm; through 10, some retraction of extended arm with flexion of the wrist; and through 11, with current increasing to 1 volt, no action of arm, but slight contraction of trunk. The experiment upon the opposite side was incomplete, because of damage to one of the nerves, but the partial results were in conformity with those obtained contralaterally.

The cord of a second, large animal was exposed between nn. 4 to 8 inclusive. Stimulation of the dorsal roots of nn. 4 and 5 resulted in ipsilateral contraction of

m. levator scapulae; of n. 6, protraction of brachium and flexion of antibrachium on both sides; of n. 7, largely as last, but ipsilaterally only and with more retraction; and of n. 8, ipsilateral retraction of arm, with retraction of both hind legs and curvature of tail to that side. Stimulation of the ventral roots after cutting the dorsal roots resulted very similarly, except that through n. 8 there was more extension of the forearm.

This experiment suggests that the dorsal roots of all the brachial nerves carry x-afferent fibers, the action resulting from their stimulation matching to a large degree the effect of stimulation of the corresponding ventral roots, with the exception that those of n. 6 are almost equally contralateral in action, and those of n. 9 almost exclusively so. The more peripheral experiment also tends to verify the latter statement. In addition, at least the first of the thoracic nerves posterior to those contributing to the plexus carries x-afferent fibers to connect with motorneurons of the contralateral member. Stimulation of the ventral or motor roots obtained results essentially similar to those performed more peripherally, as already described, except that they suggest that n. 10 carries axons only to the flexor musculature of the distal part of the limb.

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THE HALOPHYTE PROBLEM IN THE LIGHT OF RECENT INVESTIGATIONS

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INTRODUCTION

DURING the last few years considerable advances have been made in our knowledge of the conditions under which the halophytes exist. Until a short time ago the halophyte problem was approached purely from the morphological aspect, and there was no information available providing quantitative data about the environmental conditions and the physiological constitution of the different plants. Morphological investigation has shown that there is a considerable variation in structure among halophytes: there are the succulents, e.g. *Salicornia* spp.; grasses, some of which have salt-excreting glands, e.g. *Distichlis*; plants delicate in structure and which remain nearly always submerged, e.g. *Zostera*; and plants with no apparent special halo-combating mechanism, e.g. *Juncus Gerardii* and *Phragmites communis*. Some species that occur in haline communities also may be found in other habitats. *Phragmites communis* may be cited as an example occurring in fresh water and also on dunes (Voorne in Holland). A possible explanation in these cases may be the existence of different physiological races. This is a possibility that has not yet been examined but an autecological investigation should contribute to its elucidation.

In the last few years papers have appeared with a profusion of facts about the environmental conditions and physiological reactions of the halophytes of salt marshes and of the salt deserts. As a result of these papers a new outlook on the halophyte problem has been introduced, an outlook rendered valuable by the fact that it rests upon measurements made under field conditions or under conditions that approximate to those in the field. We are still a long way from complete knowledge of the why and wherefore of halophytes and it seems increasingly evident that future research must be a combination of autecology and physiology.

HALOPHYTES AND SOIL SALINITY

The structure and existence of halophytes do not seem to be entirely separable from their actual distribution. Factors that influence the distribution by bringing about a physiological response from the plant must also be of importance to the general problem of halophytism. It has long been suggested that the distribution of halophytes is determined by the salt concentration of the soil solution, and therefore recent work along these lines should be of singular importance. In all these researches it is important to appreciate the fact that there is no adequate method of determining the absolute salt concentration of the soil. If the soil sample is leached with water and then titrated with silver nitrate there are at least two sources of error: one cannot be sure that all the chloride is removed by leaching as some may have been absorbed by the soil colloids; secondly, the result gives the total chloride content and pro-

vides no information about the metallic ion. To secure this information a separate analysis is necessary. In general, the bulk of the chloride can be regarded as sodium chloride, but at the same time it is evident from recent work (cf. Baas-Becking [1]) that in some cases the metallic ion may be of importance. This work, however, has been carried out chiefly on elementary organisms (e.g. *Dunaliella*) and it remains to be seen how far it will be applicable to the phanerogams.

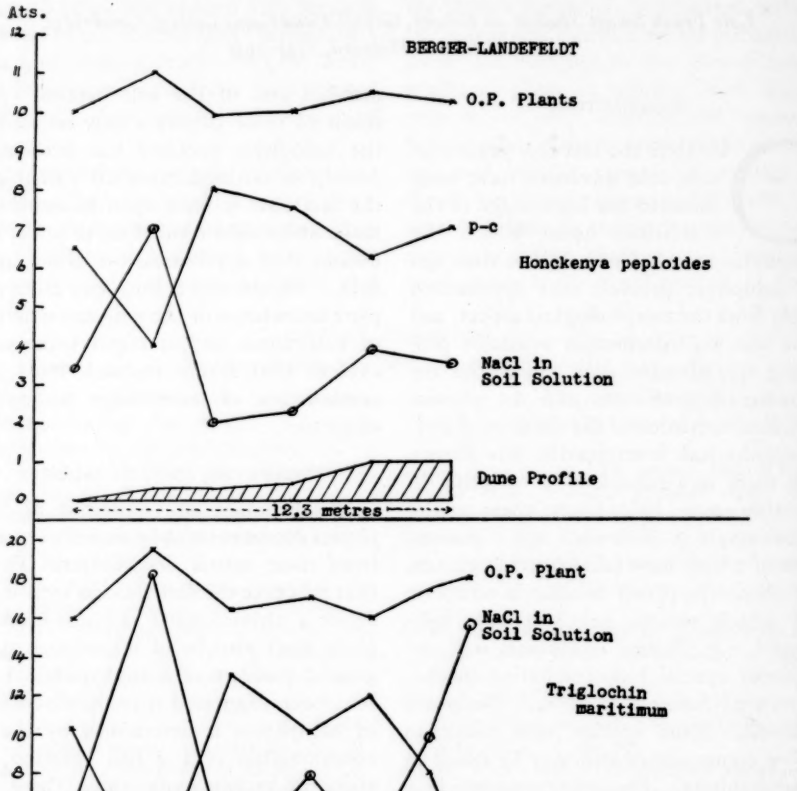


Diagram 1. (After Berger-Landefeldt)

a) Dune and salt marsh halophytes

Berger-Landefeldt [2] has recently investigated the changes of salinity that

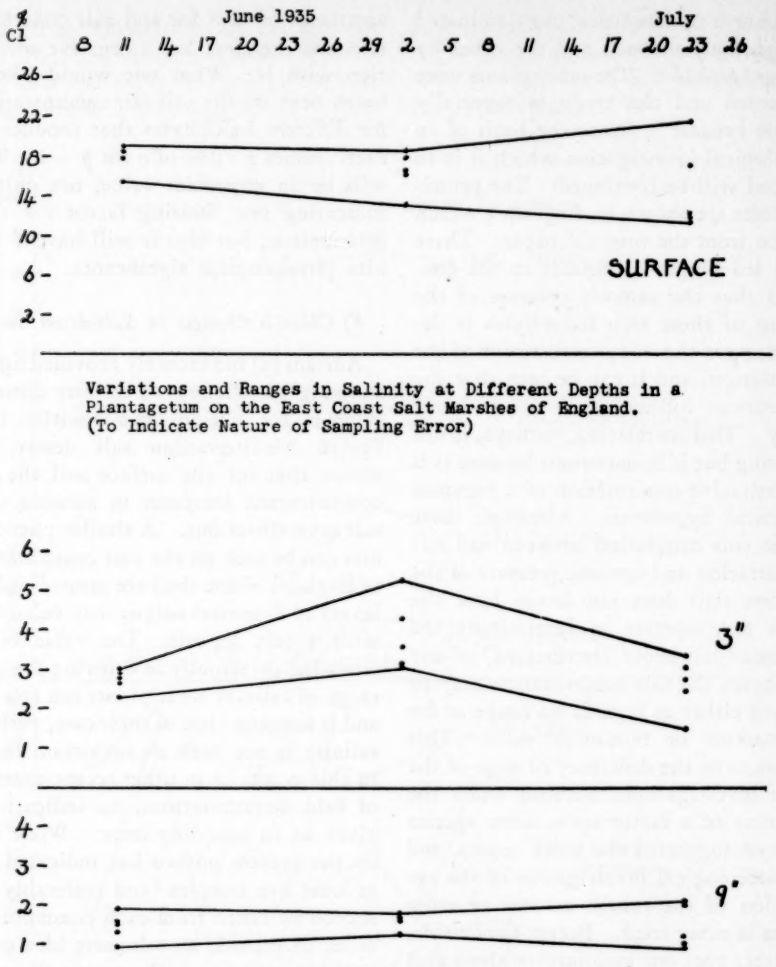
occur in two communities, one dominated by *Triglochin maritimum* and the other by *Honckenya peploides*. The other plants were disregarded and the study is especially valuable because it forms the basis of an autecological investigation which it is to be hoped will be continued. The principal results are shown in diagram 1 which is taken from the original paper. These results led Berger-Landefeldt to the conclusion that the osmotic pressure of the cell sap of these two halophytes is dependent upon the salt concentration of the soil solution, and it can be seen that the two curves follow each other fairly closely. This correlation, perhaps, is not surprising but it is important because it is a quantitative confirmation of a previous theoretical hypothesis. Although there may be this correlation between soil salt concentration and osmotic pressure of the sap, one still does not know how the former may operate in determining the existence (and hence distribution) of any halophyte: the salt concentration may be limiting either as regards its range or for a maximum or minimum value. This appears to be the deficiency of most of the recent investigations, because when the operation of a factor upon some species has been suggested the work ceases, and the autecological investigation of the application of the results to one or more species is never tried. Berger-Landefeldt, however, goes one step further along this line of enquiry. He investigates the values for $p - c$, where p = o.p. sap and c = o.p. soil solution. The significance of this function lies in the fact that when $p - c$ is a maximum the cells are turgid, the plants are healthy and growth is good. When $p - c = 0$ he suggests that the plants are at the condition usually termed the 'wilting point'. It will be seen from diagram 1 that the curve for $p - c$ is the antithesis of that for soil salt concentration and therefore has a negative correlation with it. What one would like to know next are the soil salt concentrations for different halophytes that produce for each species a value of 0 for $p - c$. This will be an important value, not only in indicating one limiting factor for their distribution, but also it will have a definite physiological significance.

b) Chloride Changes in Salt-desert Soils

Adriani [3] has recently provided figures showing the changes of salinity during a summer for various communities in a French Mediterranean salt desert. He shows that for the surface soil the salt concentration increases in summer until salt crystallises out. A similar phenomenon can be seen on the east coast marshes of England where the bare ground and the leaves of *Limonium vulgare* may be covered with a salt deposit. The value of his work lies principally in showing the great range of salinity some plants can tolerate, and it suggests that in their case, perhaps, salinity is not such an important factor. In this work, as in other recent examples of field determinations, no indication is given as to sampling error. Work done by the present author has indicated that at least five samples (and preferably ten) should be taken from each community in order to provide an adequate idea of the possible variation. Diagram 2 illustrates the nature of the sampling error for salinity in an English salt marsh community.

c) Variations in salt concentration

Schratz [4] has carried out experiments upon certain halophytes by growing them in salt-solutions of varying concentrations. As a result of his experiments he has been able to show that by increasing



Variations and Ranges in Salinity at Different Depths in a Plantagetum on the East Coast Salt Marshes of England. (To Indicate Nature of Sampling Error)

Diagram 2

the salt concentration from o per cent to 0.6 per cent

(1) The total water consumption per fresh wt. is increased.

(2) Transpiration per fresh wt. is lowered.

(3) There is an increase in fresh wt. gain of the plant per unit period of time. (o — .3 per cent NaCl only.)

(4) Productivity of the transpiration current is raised.

By this latter is meant

$$\frac{\text{Increase in fresh wt. of plant}}{\text{Total water uptake}}$$

Whether one is justified in regarding this ratio entirely as a product of the transpiration current is not argued. Diagram 5a, for *Plantago coronopus*, reproduced from Schratz's paper, shows the kind of results he obtained, and it will be noticed that the maximum difference in fresh wt. gain occurs at the flowering period. It is interesting to note that for fresh weight gain and productivity 0.6 per cent NaCl appears to have a depressant effect, and in this connection it must be pointed out that the salt concentrations used by Schratz are low compared with values which have been recorded from halophyte habitats elsewhere (the present author has recorded values up to 27 per cent, cf. below). One wishes, therefore, that the effects of still higher concentrations had been studied as giving a truer picture of the conditions under which halophytes exist. At present one does not know much about the behavior of the plants at higher chloride values. Schratz suggests that the chloride may operate upon halophytes in three ways:—

(1) Lowers the total water need by decreasing transpiration, reducing surface development and ultimately reducing the whole evaporating surface.

(2) Increasing fresh wt. gain by raising the productivity of the transpiration current. This holds good only for low values of NaCl. At the same time Schratz suggests that ecologically this is the most important effect, but again it must be stressed that his salt concentrations appear to be lower than those occurring naturally, and this fact tends to neutralise the importance of the suggestion.

(3) The salt taken in by the plant regulates the O.P. of the sap and also the acidity of the sap.

d) Early stages of development and salt concentrations

Seed germination.—Schratz [4] has tried the effect of different salt solutions on the germination of seeds of *Lepidium sativum*, *Sinapis alba*, and *Aster tripolium*. The latter came from two habitats, one haline, the other non-haline. His results showed that there is no fundamental difference between the saline *Aster* and the others. The general effect at high concentrations (1.18 per cent salt, whereas Montfort has recorded 2.3 per cent for *Aster* and the present author 6.7 per cent) is to delay the start of germination, but once started it proceeds at a greater rate so that after about 17 days there is no marked difference in per cent germination with per cent salt concentration.

Seedling development. The effect of salt upon the development of seedlings of a few species was investigated by Montfort and Brandrup [5]. Their principal conclusions are summarised in the schematic diagram below. The optimum salt concentrations found for development were—

Aster tripolium: fresh water — .39 per cent salt

Salicornia herbacea: about 2.5 per cent salt

This investigation must be regarded as autecological and of great importance. It demonstrates that the salt concentration of the surface soil in the spring is a potent factor, and it suggests that this seasonal salt concentration may be one of the ultimate factors determining the distribution of these two species. It also indicates that seedlings may respond in a different way than the adult plants to the environmental factors. Montfort, for example, never records a salinity for *Aster* in the seed region of the soil lower than 0.52 per cent. This suggests that, in general, *Aster* seedlings do not germinate in nature

under optimum conditions. I have obtained some confirmation of these results by growing plants of *Aster tripolium* in salt marsh soil watered (a) with sea water (b) with fresh water and (c) in garden soil watered with fresh water. The plants did best in (c) and died in (a). The final salinities were (a) 18.63 per cent (b) 2.68 per cent (c) 1.47 per cent chloride.

These results show that an intensive study for a year of the habitat factors of *Aster* and *Salicornia* would probably yield extremely valuable results. In European salt marshes *Aster tripolium* usually occurs at low levels next to the *Salicornietum*, and

e) Maximum salinities

The following figures have been collected from various sources and serve to indicate the high concentrations that some species are capable of tolerating.

	% Chloride Surface		
	Max.	*Min.*	*Root region*
Aster tripolium.....	12.8	0.52	6.61
Salicornia herbacea.....	6.9	1.9	....
Triglochin maritimum....	12.8	0.38	6.61
Phragmites communis....	12.8	....	6.61
Scirpus maritimus.....	3.78	0.14	2.48
Bare ground.....	20.00	5.8	....

In addition, the present author has records of *Samolus valerandi*, *Phalaris arundinacea*, and *Oenanthe peuceudanifolia* growing in salt concentrations between 2 – 4 per cent.

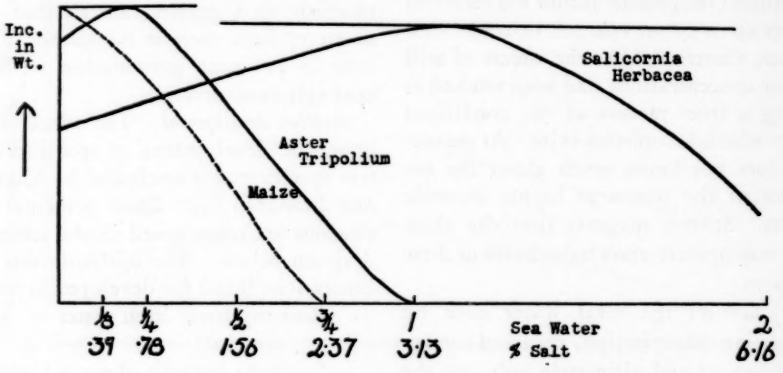


DIAGRAM 3 (After Montfort)

in view of the great differences in salinity toleration exhibited by *Aster* and *Salicornai* respectively a knowledge of any seasonal fluctuations in soil salinity appears important. It is extremely striking that a species such as *Aster*, which usually grows at low levels on salt marshes and is inundated by tides frequently, should show its optimum growth in fresh water conditions. It is by the investigation of such a species, growing in true haline conditions and yet flourishing best in a glycophytic medium, that one can hope for a considerable advance on our knowledge of halophytes.

HALOPHYTE HABITATS

As a result of his investigations into soil salt concentration in relation to different halophytes, Berger-Landefeldt [2] distinguished two types of halophyte habitat. The first he termed the xero-haline and the second the hygro-haline. The characteristics of the former habitat are that it is very dry, has a low salt concentration, and the plants have a low osmotic pressure and usually possess deep

roots. One of the principal difficulties would appear to be to determine that salt concentration at which any given habitat becomes haline, and it might be legitimate to ask whether the xero-haline habitat really should be regarded as truly haline. The hygro-haline habitat is moist or very wet and has a high salt-concentration. There is usually a ready flow of salt water and the plants are typified by comparatively high osmotic pressures, 15–20 atmos. This classification of halophyte habitats is used also by Steiner [6] who considers subdivisions of the hygro-haline type which will be referred to later. It is probably too early yet to say how far this division is going to be satisfactory and much more data are required. If the generalisations of Berger-Landefeldt hold good then it seems as if we have been provided with a real contribution towards the halophyte problem. Autecological studies of hygro-haline and xero-haline plants should lead to a much better understanding of the general halophyte problem.

OSMOTIC RELATIONSHIPS OF HALOPHYTES

a) Osmotic pressure of Surface Soil

Steiner [6] has recently investigated the relation of the distribution of salt marsh vegetation to osmotic pressure of the soil. He found that it varied over short distances horizontally and these variations could be correlated with the distribution of the dominant species. The type of result he got is depicted in diagram 4.

In connection with these results, however, it is necessary to point out certain facts. Although the soil osmotic pressure may show these variations, at the same time one cannot say it is due to any one salt in the soil. The cryoscopic method of determination employed involves all the soluble salts in the soil solution and one does not know which is the dominant component. It would be interesting to have had the figures for chloride concentration for comparison. Further, Steiner's paper gives no clear indication of the sampling error. This may be considerable and it has already been shown that the chloride range tolerated by one species may be very wide, and unless there is any compensating action by the other solutes then the O.P. of the soil would also vary.

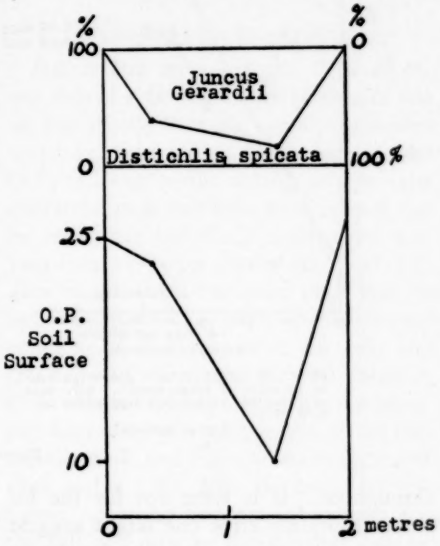


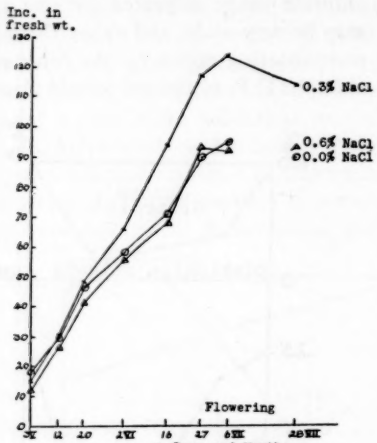
Diagram 4
(After Steiner)

Unless one knows the maximum range of the O.P. in a given area one cannot tell whether the observed fluctuations have any significance or not. Steiner's results are full of interest but their interpretation requires caution in view of these possibilities.

b) Changes of O.P. with depth

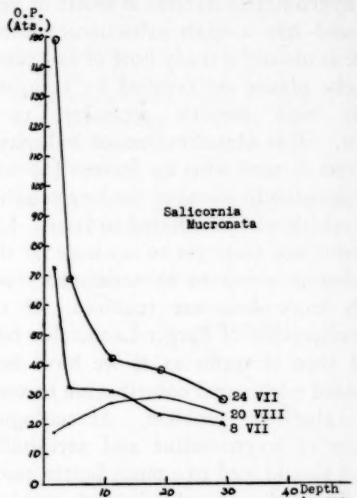
This information is also provided by Steiner and must be subject to the limita-

tions already mentioned. The curves for *Distichlis spicata* and *Spartina glabra* are similar to those reproduced for *Salicornia mucronata* (diagram 5b). The other four species investigated showed little change with depth and had low O.P. values throughout. If it were not for the inherent sampling error one might suggest that these four species are intolerant towards high osmotic pressure or great variations in osmotic pressure of the soil solution. The habitat of *Salicornia mucronata* shows the most extreme ranges and the tolerance of this species to such conditions suggests why it is a successful pioneer. The same applies to *Spartina glabra* and *Distichlis*, but to a lesser extent as their range is not so great.



Effect of different salt concentrations on increase of fresh weight. Note peak at flowering period and depression in 0.6% NaCl.

(After Schratz) a.



Osmotic change in relation to soil depth. Note leaching effect of the autumn rains in curve for 20 VIII.

(After Steiner) b.

Diagram 5

c) *Variations in O.P. of the soil*

The changes of the *Salicornia mucronata* habitat are shown in diagram 5b reproduced from Steiner's paper. This shows the great variation and also the effect of the autumn rains (Curve 20 viii). *Spartina glabra* and *Distichlis spicata* behave similarly, whilst the other species (*Juncus Gerardii*, *Spartina patens*, *Salicornia herbacea*, and *Iva oraria*) show little or no change with season. The leaching effect of rain is also shown by the following set of figures.

Species habitat	O.P. in ats. 24 VI (*before*) *rain.*	2 VII (*after*) *rain.*
Spartina glabra	33.5	28.5
Spartina patens	25	21
Distichlis spicata	22	16.7
Juncus Gerardii	18.9	6.7
Salicornia europaea	40–45	4.3

Diurnal changes are provided by the following figures:—

Time	*Salicornia herbacea*	*Distichlis*	*Spartina patens*	*Juncus Gerardii*
8.30	149.4	106.8	31.1	28.7
17.40	198.0	155.0	39.1	28.8

In both these sets of figures no allowance appears to have been made for the sampling error nor can one tell which of the soil

salts had changed most in concentration. It is possible that the diurnal changes are covered by the sampling error. What one would really like to know is the maximum change that can occur in one day during any part of the year. It is also probable that the maximum and minimum values are of more significance than the daily change.

In addition to the changes described above, Steiner says that temperature and hour after flooding (salt marsh) also affect the O.P. of the soil, but he does not provide any figures or give any indication of the value of the variations.

d) Osmotic pressure of cell sap and soil

Adriani [3] has declared that the osmotic pressure of cell sap is higher for plants living in the more saline soils, and that it can also be correlated with the salt content of the soil. The greatest range found in the Mediterranean was shown by *Obione portulacoides*, 22–105 Atmos. In this connection it must be pointed out that a correlation between O.P. cell sap and the salt content of the soil should depend upon the relative proportion of NaCl in the soil in relation to the other soluble salts.

e) Variations in O.P. cell sap of the Halophytes

When the variations in O.P. of the sap are investigated during the growing season it is found (Steiner) that the halophytes can be grouped into three classes depending on their behavior.

I. O.P. cell sap fluctuates with rainfall. In dry weather the O.P. rises and in wet weather it falls. This is shown in diagram 6I, where *Spartina glabra* is a typical example.

II. The alterations in O.P. sap are, in general, an expression of displacements in water content. The changes reflect those of all the O.P. components and not that of Cl^- only as in group I. *Solidago sempervirens* is an example. (Cf. diagram 6II.)

III. There is no relation to the external conditions. The O.P. shows a relation with the Na^+ and Cl^- components and the salt taken in forms the controlling mechanism. The best example of this group is *Juncus Gerardii*. (Cf. diagram 6III.)

MAXIMUM OSMOTIC PRESSURES

Steiner has measured the O.P. of the cell sap of a large number of species and he has shown that the osmotic pressures may vary from 13–48 atmospheres. The O.P. cell sap is due to the soluble salts contained in it and from his figures it can be seen that the NaCl component may vary from 18–85 per cent of the total O.P. This makes it all the more important to know the percentage effect of the different components that determine not only the cell sap O.P. but also the soil solution O.P. Unfortunately Steiner has not given any figures for the components of the soil solution O.P. and this materially decreases their value. He also indicates by his figures that the Sodium component for the cell sap may be greater than can be accounted for by the chloride. In the case of *Spartina glabra* the Na^+ component accounts for 25 Ats. of the total and the chloride for only 17 Ats. (Cf. also diagram 6IV).

The following table indicates the maximum values for the soil solution O.P. and also the range of variation.

Species	*Surface (Ats.)*		*Root (Ats.)*	
	Max. value	*Variation*	*Max. value*	*Variation*
Salicornia mucronata.	198	182	60	30–40
Spartina glabra.....	147	130–25	29	2
Distichlis spicata...	155	72– 7	24	3– 2
Spartina patens.....	31	18–10	21	1
Juncus Gerardii.....	29	17– 6	24	3– 1
Honckyena peploides..	10.88	11	..	....
Triglochin maritimum	19.64	3– 7	..	....

From these figures it is clear that *Juncus Gerardii* and *Spartina patens* differ from the other three in the surface conditions but when the root area is concerned it is *Salicornia mucronata* that differs from the rest. Biologically, changes in the root region will be more important and hence more significant.

	Soil. 0–5 cms.	*Sap.*
Shaded	60.2 Ats.	53.9 Ats.
Partly Shaded	58.9 Ats.	27.3 Ats.
Unshaded	42.1 Ats.	32.3 Ats.

This suggests a correlation between soil and sap O.P. but it must be remembered that no allowance is made for sampling error, so that there is no indication of the

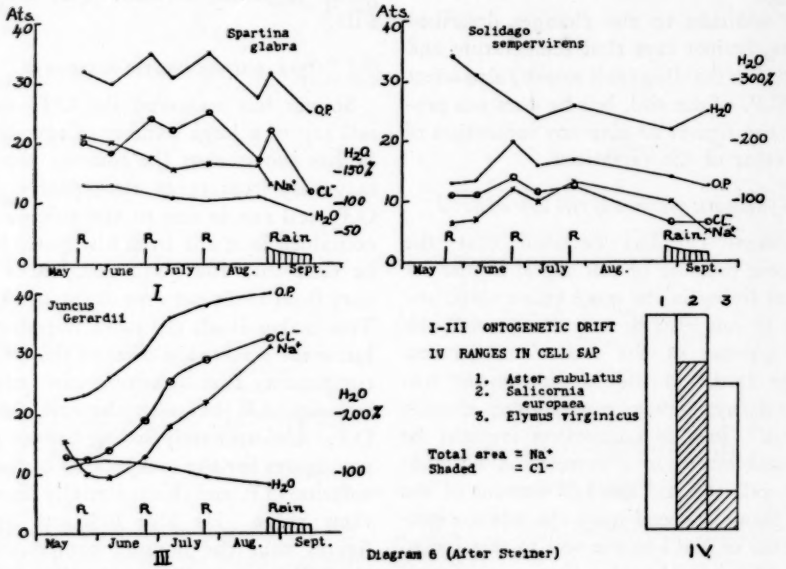


Diagram 6. There are 3 groups ontogenetically:—

I. O. P. shrinks with rainfall. Dry means a rise; wet means a fall.

II. The trivial alterations in O. P. are, in general, an expression of displacements in water content. Changes in O. P. reflect those of all components.

III. No relation with weather. There is a definite relation with NaCl content, and the salt taken in is the controlling mechanism.

SALICORNIA HERBACEA

It has been suggested earlier that autecological studies of one or two halophytes might lead to useful conclusions. In support of this thesis a short survey will be made of the known facts relating to the so-called *Salicornia herbacea*, such facts being gathered from a number of recent papers. Steiner [6] has obtained some figures for the osmotic pressure relations. possible range under the different conditions. Steiner concludes that the optimal development is inhibited in a habitat poor in salt, whilst a very high salt content produces a stumpy form and may cause death. He further concludes that the optimum development of the species is determined by the light value. In 1915 Johnson and York [7] suggested that at high levels soil moisture content determined the existence of the plant whilst at

low levels length of submergence was the dominating factor. This idea has been carried a stage further by Wiehe [8] who has shown that under certain physiographic conditions submergence may act mechanically at low levels by uprooting the seedlings.

Wiehe does not, however, provide any data about salinity changes etc. but at the same time his work suggests that *Salicornia* might exist under certain conditions but that it is prevented from doing so by mechanical forces. Work by the present author (unpublished) on salt marshes of east England leads one to conclude that submergence may be an important factor, but that other factors are probably involved as well. Montfort and Brandrup [5] have shown that the salinity for optimum development is 2.5 per cent whilst the range for the species appears to be between 6.9 per cent and 1.9 per cent. From a survey of the various papers a list of the principal factors which appear to influence the growth and distribution of this species can be drawn up:

a) Number of submergences
b) Length of non-tidal exposure (a period of one or more days during which no tide covers the area)
c) Salinity
d) Soil moisture
e) Competition.

Although all these suggestions have been made by various authors it is to be regretted that no field experiments have been carried out to prove these hypotheses. One of the objects of this survey is to show that there is plenty of information but that it wants collating for each species, and then a series of field experiments devised and carried out to prove the various suggestions.

OSMOTIC VEGETATION OF HYGRO-HALINE HALOPHYTES

As a result of his observations on osmotic pressure Steiner [6] has suggested that there are three types of regulatory mechanism for O.P. of hygro-haline halophytes.

I. Succulence. Their osmotic changes are compensatory. When there is an increase in the salt content of the sap there will be a dilution from the water store, e.g. *Iva ovaria*, *Plantago maritima*, *Salicornia* spp.

II. 'Absalzende' forms. There is no permanent rise in the O.P. because any salt accumulation is controlled by the salt removing glands. Examples:—*Spartina* and *Distichlis*.

III. No regulatory mechanism. The maximum peak of the O.P. rise marks the end of the vegetative period. e.g. *Juncus Gerardii*.

In the light of these conclusions the structure of halophytes takes on a new interest and their morphological characters assume a physiological significance.

CONCLUSION

The results of recent researches indicate that the halophyte problem is concerned with a number of environmental factors. Future investigations, it would seem, must be concerned with how and when these factors operate. It is necessary to know which season of the year is vital and which part of the plant life cycle is most affected, and what particular organ of the plant receives the stimulus. It is also essential to have information concerning the greatest range for a factor that any given species can tolerate. Finally such conclusions as are reached require to be tested by field experiments, which up to the present have not been numerous. Finally,

it cannot be stressed too strongly that autecological studies of different halophytes combined with physiological experiments, would probably lead to considerable advances in our knowledge of their behavior and mechanism.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

RACE, SEX, AND ENVIRONMENT. *A Study of Mineral Deficiency in Human Evolution. By J. R. de la H. Marett. Hutchinson and Co., London.* 21 shillings net. 9 x 6; 342; 1936.

An interesting theory of human evolution. The author's conception is that mineral deficiencies of the soil and the resulting vegetable food have influenced animal and human evolution. Chapter I deals with the general problem. The next four chapters "contain some of the more important ecological and physiological facts that are intended to supply means for the formulating and checking of the theories of physical and social evolution constituting the remainder of the book. This main object is to trace the distribution of the more important minerals, together with their effects outside the human body; and in particular to determine which of them are abundant and which rare as a result either of aridity or of humid conditions." An attempt is then made to envisage the kind of physiology best suited to each special environment. In the remaining eleven chapters the theories presented are applied to the problem of human evolution. The author believes that mineral deficiency has influenced selection both for bodily and for mental characters, some of which appear to have become linked even before the emergence of the vertebrate on to the land. Considerable space is given to a discussion of the origin of man, also to a hypothesis whereby mineral deficiency is credited with the power of removing or simplifying characters whose over-specialization might otherwise have prevented further and alternative adaptation. Mineral deficiency is also held responsible for a series of arrests of bodily growth, during each of which the relative size of the brain to the body has been increased.

The author confesses that his researches have raised many more questions than he has been able to answer. These enter not only the domain of the anthropologist but that of the geologist, the soil chemist, the geneticist, the physiologist and the psychologist. All workers in these fields will find this a stimulating book. It is documented and contains a glossary, and an author's and subject index.

ÉVOLUTION DE L'ATMOSPHÈRE. *Circulation Organique, Époques Glaciaires. Actualités Scientifiques et Industrielles 271. Exposés de Biométrie et de Statistique Biologique, VIII. By V. A. Kostitzin. Hermann et Cie, Paris.* 10 x 6½; 46; 1935 (paper).

This is an attempt to express in a generalized mathematical form the variations in the quantity of oxygen, carbon (CO_2) and nitrogen present on the earth; and the relation of these variations to vital phenomena. A system of differential equations is used to represent the interchange of the above elements between the atmosphere, lithosphere and hydrosphere and in relation to the metabolism of plants and

animals. The equations are simple and their characteristics are briefly analyzed. The author proceeds then to re-examine the hypothesis of Arrhenius regarding the origin of the glacial periods. As it is recalled, Arrhenius attributed the appearance and disappearance of glacial periods to the changes in the quantity of atmospheric CO_2. Our author overcomes the numerous objections to the hypothesis of Arrhenius by extending his equations to include variations in the activity of volcanoes and in the vertical movement of the earth's surface. The resultant equation, according to the author, satisfies the requirements necessary to explain the localization and periodicity of glaciation.

As the author admits, this is only a first approach to the mathematical analysis of the variations of the three elements and of the consequences of these changes. It will be interesting to note at what less generalized derivations the method will arrive.

L'Espèce.

By L. Cuénot. Gaston Doin et Cie, Paris. 30 francs. $8\frac{3}{8}$ x 6; 310; 1936 (paper).

To the age old question—What is a species?—the eminent French biologist seeks an answer by enlisting the aid of modern genetics. He first re-examines the classical definition and traces its historical origin, then discusses the terminology introduced by the modern taxonomists. After a concise and clear exposition of the principles of genetics, the author describes the morphologic and physiologic characteristics, the genetic constitution and the ecology of some 30 "species" of plants and animals. With the emphasis on the genetic characteristics, he discusses and criticizes the basis of the classification given the "species" in question. From these and other general considerations he concludes that the classical definition of species enables the systematist to group most varieties of plants and animals. For the remainder, he proposes some general rules which he illustrates with concrete examples. From this study, it becomes evident that we are yet far away from a classification which can be consistent and objective. Teleologic concepts still persist and apparently there are some who find it difficult to differentiate between the object and its name. The author's critical analysis should contribute much towards a more precise terminology.

Vérifications Expérimentales de la Théorie Mathématique de la Lutte pour la Vie. *Actualités Scientifiques et Industrielles, 277. Exposés de Biométrie et de Statistique Biologique, IX.*

By G. F. Gause. Hermann et Cie, Paris. 18 francs. 10 x $6\frac{1}{2}$; 63; 1935 (paper).

This small volume can be looked upon as an extension and experimental elaboration of certain of the ideas developed by Doctor Gause in his recent book, *The Struggle for Existence* (reviewed in Q. R. B. June 1935). In the present volume the author discusses the following three types of biological associations: first, the competition between two species in the same ecological niche for the same food; second, the competition between two species in different ecological niches for the same food, and, third, the predator-prey situation where one species lives at the expense of the other. The experiments illustrating the first relationship are based on competitions between *Paramecium aurelia* and *P. caudatum*; the second relationship is illustrated with *P. caudatum* and *P. bursaria*, and the third with *P. bursaria* (predator) and *Saccharomyces exiguus* (prey).

This book forms an interesting addition to the field of experimental populations although it does not add greatly to the theoretical ideas developed by the author in his earlier volume; in fact it should be used as an appendix to the latter work. There is a brief bibliography and several text illustrations.

Einführung in die Palaeontologie.

By Hermann Schmidt. Ferdinand Enke, Stuttgart. 15 marks (paper); 16.80 marks (cloth). 10 x $6\frac{1}{2}$; 253; 1935.

An introduction to paleontology with chapters devoted to the animal forms in

ascending order, followed by a chapter on plants and three others treating paleobiology, biostratigraphy and methodology, respectively. A short bibliography of selected titles and an index of animal and plant names are included. A good textbook, whose usefulness, however, will be largely confined to German schools.

ENVIRONMENT OF THE EARLY VERTEBRATES, *by Alfred S. Romer and Brandon H. Grove.* SUMMARY OF UPPER DEVONIAN STRATIGRAPHY, *by George H. Chadwick.*

American Midland Naturalist, University of Notre Dame, Notre Dame, Indiana. 30 cents. 9 x 6; 57; 1935 (paper).

The major portion of this treatise is devoted to a description and summarization of habitats of early vertebrates found in North American pre-Carboniferous material. For purposes of study the investigator groups the various finds into four classes, 1–4, in order of their gradation from fresh to salt water conditions of deposition. Conclusions derived from analysis of this material unquestionably indicate that fish history commences in fresh waters.

BULLETIN OF THE BUFFALO SOCIETY OF NATURAL SCIENCES, *Volume XVII, No. 1. New Fossils from the Western New York Devonian.* Containing following articles: *Some New Forms and New Occurrences of Fossil Plants from the Middle and Upper Devonian of New York State*, by Chester A. Arnold; *Pseudohydnoceras, a New Hamilton Dictyosponge*, by Irving G. Reimann; *New Upper Devonian Fishes from Western New York*, by William L. Bryant; *New Species and Some New Occurrences of Middle Devonian Blastoids*, by Irving G. Reimann.

Buffalo Society of Natural Sciences, Buffalo. $9\frac{3}{4}$ x $6\frac{1}{2}$; 45 + 4 plates; 1935 (paper).

GENETICS

THE BEGINNINGS OF PLANT HYBRIDIZATION *By Conway Zirkle. University of Pennsylvania Press, Philadelphia.* $2.50. 9 x 6; xiii + 231 + 8 plates; 1935.

Unfortunately, in the brief space allotted, it is only possible to indicate a few of the many interesting features of this book. The author has made a painstaking investigation of all the known literature pertaining to plant hybridization before Koelreuter. A brief survey of ancient and medieval beliefs concerning hybridization is given, concluding with John Ray who in his sermon on natural theology about 1660 anticipated Darwin's pangenesis hypothesis and described alternate or Mendelian inheritance of human hair color. The first real intimation that hybrid plants could be secured by cross pollinations seems to have come from Camerarius. In this country the Indians long recognized the tendency of different types of maize to mix. The author quotes in full from the original sources of the early descriptions of xenia and gives a reproduction of the earliest Mendelian segregation as illustrated by Jakob Theodor of Berg-zabern (Tabernaemontanus).

Accurate accounts of plant hybridization date from the first half of the eighteenth century. The first record is by Cotton Mather in 1716, then follow such names as Thomas Fairchild, Richard Bradley, Jean Marchant, Thomas Knowlton, Philip Miller, Paul Dudley, and many others, down to and including Linnaeus. Of the utmost importance to the reader will be the reprinting, usually in full, of the original writings of these men. In the final chapter is given a résumé of later hybridization. The volume contains a number of illustrations, a lengthy bibliography and a detailed index.

GENETIC VARIATIONS IN RELATION TO EVOLUTION. *A Critical Inquiry into the Observed Types of Inherited Variation, in Relation to Evolutionary Change.*

By H. S. Jennings. Princeton University Press, Princeton, N. J. $2.00. $8\frac{1}{2}$ x $5\frac{1}{2}$; iv + 139; 1935.

This volume is based on a series of lectures given at Princeton University in 1934. The topics discussed in the five lectures are as follows: I. Structure of the germ

plasm. Genetic variations resulting from new combinations of genes; II. (1) Genetic variations resulting from irregularities in the structure and operation of the genetic system. (2) Gene mutations; III. Are the gene mutations observed in experimental genetics the basic material of progressive evolution?; IV. Genetic variation in unicellular organisms, with special relation to the inheritance of environmental effects and reactions; V. Genetic variation in unicellular organisms, continued. What is the method of operation of the genetic system in bringing about genetic variations under the long-continued action of environmental conditions? A book of interest to all biological students and teachers of biology in universities, colleges, and secondary schools. It is illustrated and to each chapter is appended a series of notes and references. There is no index.

LES CONCEPTIONS MODERNES DE L'HÉRÉDITÉ *By Maurice Caullery. Ernest Flammarion, Paris.* 15 francs. $7\frac{1}{2}$ x 5; 312; 1935 (paper).

This is an unusually clear exposition of the fundamentals of genetics. The author summarizes the most important investigations on the subject, both experimental and statistical, and interprets the findings in terms understandable by the layman. Very little is omitted and in fact this little volume is more comprehensive than many a textbook. A noteworthy feature is the excellent perspective of the author in evaluating the contribution of each geneticist. While the work on Mendelian inheritance receives the most attention, yet the author has not neglected the non-Mendelian forms. The bibliography is sufficient.

GENERAL BIOLOGY

TRANSACTIONS OF THE BOSE RESEARCH INSTITUTE, CALCUTTA. *Vol. IX, 1933–1934. Biological and Physical Researches. Edited by Sir Jagadis Chunder Bose. Longmans, Green and Co., New York.* $7.20. $8\frac{3}{4}$ x $5\frac{1}{2}$; iv + 210; 1935.

This volume deals with the following biological subjects. I. Modification of vital activity after inflorescence in *Mimosa pudica*, by S. C. Das and B. K. Palit. The appearance of inflorescence induces a depression of moto-excitability of the pulvinus. The velocity of excitatory impulse in the petiole of the leaf also undergoes appropriate variation at inflorescence. II. Periodic variation in longitudinal and diametric growth of stem in *Helianthus*, by S. C. Das and B. K. Palit. Special devices are described which give automatic records of the simultaneous variation of both longitudinal and diametric growths throughout a complete cycle. The results are given in detail. III. Automatic record of embryonic growth on germination of the seed, by B. K. Dutt and A. Guha-Thakurta. By means of the automatic apparatus herein described the actual moment of germination inside the seed of *Cicer arietinum* is determined; also the rate of growth of the embryonic radicle. IV. An automatic respirograph, by A. Guha-Thakurta and B. K. Dutt. The apparatus, constructed on the principle of the photosynthetic bubbler, automatically records the rate of oxygen consumption for respiration. V. A chemical, physicochemical and physiological investigation on oil soluble vitamins in *Cicer arietinum*, by N. C. Nag and H. N. Banerjee. Kabuli chhola oil supplies all the necessary essentials for proper nutrition, healthy growth, and propagation of rat colonies. In regard to oil-soluble vitamins, Kabuli chhola, closely followed by Shona moog, is superior to all other pulses. It approaches in vitamin efficiency cod liver oil. VI. An investigation on specific bacterial action on *Gur* solution unattended by evolution of carbon dioxide, by J. P. Sircar. "From the experiments given in detail it would appear that there are certain organisms which directly produce, in *Gur* solution, acetic acid, lactic acid, formic acid and acetone without evolution of any gas." VII. The racial affinities of the Oraons, by Provash Chandra Basu. This paper reports investigations on skin color, stature and head measurements of 250 primitive Oraons (adult males) living in the north-western plateau of the Ranchi district. A brief summary of their totems

is given. Detailed measurements of four male Oraon crania in the Anthropological Laboratory of the Zoological Survey of India are also included in the study. The volume also reports investigations that have been made on the continuous spectra of hydrogen halides and of the flame spectrum of hydrogen. Each paper is documented. There is no index.

ESSAI POUR UNE CONCEPTION PHYSIQUE DE LA VIE.

By D. Calewaert. Librarie Maloine, Paris. 7½ x 5¼; 78; 1935 (paper).

This is an attempt to explain life—its origin, and biological, physiological and chemical processes—in terms of physics. According to the author the first stage in the formation of matter was the impregnation of amorphous rocks by water (formation of the crystalline state resulting in ionization) and the fifth the impregnation of amino acids by methane (the formation of the polypeptides culminating in the higher organisms).

Calewaert alleges that all matter depends for its survival on its molecular density. As measured by sera of blood, gastric juice, saliva and other secretions, a young body has a greater density than an old one, and growing older is a process of dedensification. Thus a child has a greater density than an adult, and the female (because of the additional secretions connected with lactation and menstruation) a greater one than the male. Disease occurs when the infecting organism has a greater density than the affected, and therefore physicians do well to include the administration of chemical extracts of compounds of high molecular weight in the treatment, thereby increasing the density of the sera of the affected body. By way of example, syphilis is dealt with in detail, although tumors, fevers, pregnancy and immunity are also treated. We like particularly the opening sentence of the chapter on pregnancy: "Pregnancy is a benign tumor since it is finally expelled from the maternal organism." The book is without index, but it does not need one.

COLD SPRING HARBOR SYMPOSIA ON QUANTITATIVE BIOLOGY. *Volume III.*

The Biological Laboratory, Cold Spring Harbor, Long Island, N. Y. $3.75. 10¾ x 7¾; xv + 359; 1935.

The Cold Spring Harbor symposium for 1935 was built around the general problem of the influence of light on biological phenomena. The present volume, as with the previous two (reviewed in Q. R. B. 9: p. 369 and 10: p. 344), contains the papers given by the various selected investigators on this subject at Cold Spring Harbor. The discussions following each paper, which incidentally are frequently quite extended and illuminating, are included as before in the text of the volume. Such topics as the physics of light, the kinetics of photochemical reactions, the physiology of chlorophyll, the photosynthesis phenomenon, the influence of light on behavior responses, and the effect of light on metabolism are discussed.

This volume seems to be living up to the high standard of excellence set by its predecessors and should be in the hands of the biologist interested in light processes. Many of the articles are illustrated and contain an extended bibliography.

RELIGION AND THE SCIENCE OF LIFE. *With Other Essays on Allied Topics.*

By William McDougall. Duke University Press, Durham, N. C. $3.00. 7¼ x 5; xiii + 263; no date.

In the title essay of this volume Professor McDougall traces the lines of evidence that have led him from agnosticism to religion. The purposive activities of organisms, the logical and esthetic powers of the human mind, and the results of psychical research indicate to him "that each man is not what to so many scientists he has seemed to be, a fortuitous concatenation of physical forces, but is rather a ripple of the mighty ocean of spirit, an individualized ripple, small and feeble, yet sharing in the nature of the whole and not wholly detached from it." Other essays deal *inter alia* with the need for psychical research, family allowances as a eugenic measure, and the author's experi-

ments on the transmission of acquired characters.

DESERTS ON THE MARCH.

By Paul B. Sears. University of Oklahoma Press, Norman. $2.50. $7\frac{5}{8}$ x $5\frac{1}{4}$; 231; 1935.

The author, who is now Director of the Department of Botany at the University of Oklahoma, has long been a student of the conservation of our natural resources. He has written, for the general reader, a history of the pillage and destruction in this country of our most valuable possessions—our soils, our vegetation, and our wild animal life. Not one particular class, but by and large all have been blindly doing their best, in one way or another, to wreck the balance between soil and plants and animals that had been established for centuries before the influx of the European, and had made for such an abundantly rich region. Professor Sears indicates how, by intelligent action, it is still possible to arrest the development of infertile soils, of deserts, and of arid streams. The book deserves to be widely read. It is without an index.

THE CHEMICAL CONTROL OF CONCEPTION.

By John R. Baker, with a Chapter by H. M. Carleton. Chapman and Hall, London. 15 shillings net. $8\frac{1}{4}$ x $5\frac{1}{2}$; x + 173 + 8 plates; 1935.

This is the definitive statement of the results of a series of experimental investigations on the action of various pure chemical substances and proprietary preparations as spermicides *in vitro*. Aside from practical considerations in the development of better contraceptive agents than those now available, in which the author evidently achieved a considerable measure of success, the chief interest of the book is in the critical methodology and techniques developed for the study of the physiology of spermatozoa. It is a valuable reference work for the biologist, well indexed.

THE JOURNAL OF BIOLOGICAL EDUCATION, *Vol. 1, No. 1.*

Edited by Isador Ripps. Scientific Staff: M. Jay Chanin, V. Lewitus, N. R. Lubowe, L. Ripps, J. Washton, C. Weinrib, Speiss and Washton, New York. 10 cents. $9\frac{1}{4}$ x $6\frac{1}{4}$; 32; 1935 (paper).

This little journal recently made its bow to the public with the aim of furthering the knowledge of and interest in the biological sciences. It deals briefly and simply with a wide range of subjects, such as notes on the early history of the microscope, the sea-horse, narcotic drugs and their action, health chats, etc., etc. Some of the articles are illustrated. The journal will find its chief readers among high school students and the general reader interested in all kinds of biological information.

URDEUTSCHLAND. *Deutschlands Naturschutzgebiete in Wort und Bild. Lieferungen* 13, 14.

By Walther Schoenichen. J. Neumann, Neudamm. 2 marks each. $10\frac{3}{4}$ x $8\frac{1}{4}$; Lief. 13, 1–24 + 9 plates; Lief. 14, 25–48 + 9 plates; 1935 (paper).

These two numbers inaugurate the second volume of a beautifully illustrated work treating of the nature conservation areas of Germany. This volume will be confined to the flora and fauna. The numbers comprising the first volume, on geology, have been noticed in the previous numbers of this REVIEW, beginning with Volume 10, Number 3.

ECOLOGICAL ASPECTS OF A CALIFORNIA ESTUARY.

By G. E. MacGinitie. The University Press, Notre Dame, Ind. 9 x 6; 136; 1935 (paper).

This paper presents an interesting description of a typical marine estuary of California located at Monterey Bay. The physical and biotic factors are discussed but a more valuable contribution is found in the fine catalogue of the animals with detailed natural history observations.

TRAVAUX DU LABORATOIRE DE MICROBIOLOGIE *de la Faculté de Pharmacie de Nancy. Fascicule VIII.*

Laboratoire de Microbiologie de la Faculté de Pharmacie de Nancy. 9½ x 6¼; 117; 1935 (paper).

HUMAN BIOLOGY

STUDIES OF DIFFERENTIAL FERTILITY IN SWEDEN.

By Karl A. Edin and Edward P. Hutchinson. P. S. King and Son, London. 7s. 6d. 8¼ x 5⅜; 116; 1935.

Dr. Edin's studies on differential fertility in Stockholm have been well known to students of population for a number of years. But it is of the utmost value to have available in English this comprehensive and orderly report on the progress of his work to date. It is the product of a joint effort sponsored by the Institute for Social Sciences of the University of Stockholm and the Social Science Research Council in this country.

The most striking result of the investigation is summarized as follows:

> The material analyzed consisted of records for 6,629 Stockholm families. The data were obtained by a combination of the 1920 and 1930 census returns for these families, supplemented by information from the Stockholm birth registers and family registers, and from maternity hospital records.
>
> The classification with respect to economic status was based on the 1920 income of husband, the educational status classification on the husband's degree of education as reported in the 1930 census.
>
> The observed fertility rates increased without exception from the lowest to the highest education groups. The validity of this observation was confirmed by demonstrating:—
>
> 1. that the fertility differentials were not produced by a more favorable age distribution or less frequent employment of wives in the more educated groups;
> 2. that they were not merely the result of the better economic position of the more educated;
> 3. that they were not a product of temporary changes in fertility during the post-war years;
> 4. that in all probability they were not a result of social class differences in the number of children born to wives before the observed marriages (illegitimate children plus children of former marriages).

THE MARCH OF MAN. *A Chronological Record of Peoples and Events from Prehistoric Times to the Present Day. American Editors: Albert B. Hart and Isaac J. Cox. English Editor: Lawrence H. Dawson. Encyclopaedia Britannica, New York, Chicago, London.* $12.00. 11½ x 9; 64 + 96 comparative time charts + 64 plates; 1935.

This superb reference work should be in every library, public or private, home or school, worthy of the name. It is divided into three parts. The first is a historical atlas that includes 96 plates of beautifully engraved and reproduced maps, and some 50 pages of detailed index to these maps. They begin with maps of the world as known to the ancients, and end with the world in 1935.

The second part consists of seven folding "comparative time charts of universal history," backed with linen to stand rough handling. They are printed according to an ingenious color scheme, and altogether constitute the best chronological tables we have ever seen (and we really specialize on chronological tables).

Finally the third, and least important part of the whole is a series of "historical illustrations," good enough in their way, but of no particular interest to the student or scholar.

The aid of a long array of distinguished British scholars was had by those who prepared the volume (George Philip, Ramsay Muir, and Robert McElroy for the Historical Atlas; and Lawrence H. Dawson, the English editor-in-chief, for the Time Charts). These names sufficiently guarantee the soundness of the work.

Altogether we recommend this great work, without reservation, to all and sundry.

THE BANTU TRIBES OF SOUTH AFRICA. *Reproductions of Photographic Studies. Vol. IV, Section I, Plates I–XL. The Vathonga (The Thonga-Shangaan People). With an Introductory Article on the Vathonga; a Bibliography, and Descriptive Notes on the Plates, by Henri-Philippe Junod.*

By A. M. Duggan-Cronin. Deighton, Bell and Co., Cambridge. 25 shillings net. 11½ x 8¾; 28 + 40 plates; 1935 (paper).

Volume IV, Section 1, of this anthropo-

logical study, previous volumes of which have been noticed in THE QUARTERLY REVIEW OF BIOLOGY, contains an introductory article by Henri-Philippe Junod on the Thonga-Shangaan, a tribe carefully studied and described by Dr. Henri A. Junod in his valuable monograph *Life of a South African Tribe*. In his brief survey of the present knowledge of Thonga culture he notes how under the different influences the clans have become differentiated and the resulting disintegration of tribal customs and beliefs due to European interference with Thonga life. He says: "No one can underestimate the terrific impact of our civilization on Thonga life; it is overwhelming. Nevertheless . . . the persistence of mystical and spiritual experiences in spite of our matter-of-fact view of life, the steady and growing respect of the educated Thonga for his language and his past, are sufficient proof to me that there are cultural elements in Thonga life which will survive."

There is a bibliography of 8 pages and 40 superb plates showing physical types, manner of dress, architecture, and customs.

LIFE AMONG THE LAPPS. *On the Spring Trek with the Köngämä Lapps.*

By Sven Haglund. Translated from the Swedish by William Savage. Denis Archer, London. 12s. 6d. net. 8½ x 5½; 252, 1935.

This entertaining volume gives the reader an extraordinary clear and wide ranging view of the habits, mode of life, and general philosophy of the nomad Lapps inhabiting the northern reaches of Scandinavia. They are a remarkable people. The Lapps in Sweden number about 7000. They tend over 300,000 reindeer, and get their living from them on land fit for no other use. There is no unemployment among them. As the author says it is probable that they are

tougher and more capable of resisting the weakening influences of civilisation than any other natural race, for it is only the Lapps who have succeeded in performing the difficult task of living the primitive and wandering life of the nomad within the borders of a civilised community. All other races on the same level of civilisation and culture, and living under the same or similar external conditions, have been poisoned by civilisation, its diseases and its pleasures. They have all perished, mentally and physically. The Lapps alone have been able to withstand the enormous pressure exerted upon them by Nature and civilisation.

The book is abundantly and skillfully illustrated with half-tones from the author's own photographs. It is unfortunate that it lacks any index, because in spite of its chatty narrative style it contains a good deal of useful reference material.

THE PRIMORDIAL OCEAN. *An Introductory Contribution to Social Psychology.*

By W. J. Perry. Methuen and Co., London. 15 shillings net. 8½ x 5½; xi + 380; 1935.

The aim of this book is to study some of the general principles underlying the development of human society in its various phases. The author points out that many peoples, separated by vast distances, and long periods of time, agree in the main concerning the mode of origin of their culture. This suggests that such people look back to a common source of inspiration. The early chapters in the volume are devoted to the most primitive of all peoples—the food gatherers—their fundamental innate tendencies, their behavior in family groups and the development of social institution. The creation stories, so widely held among primitive peoples, concerning the bringing up of land out of the primordial ocean undoubtedly have a definite historical basis. The author discusses at length the fundamental part which this original ocean played in the organization of the early thought of food-producing men. The latter part of the volume deals with the Origins of ideas, the Achievement of excellence and Man and society.

The volume is well documented and contains a detailed index.

ANTIQUITIES OF THE NEW ENGLAND INDIANS. *With Notes on the Ancient Cultures of the Adjacent Territory.*

By Charles C. Willoughby. Peabody Museum of American Archaeology and Ethnology, Harvard University, Cambridge. $4.75. 9¼ x 6; vii + 314; 1935.

In this volume is found a detailed account of the archeological discoveries regarding the pre-historic inhabitants of New England. The oldest remains uncovered have been attributed to the pre-Algonquin Indians who probably inhabited the region some 2000–3000 years ago. The implements found include stone-bladed adzes, semilunar knives and bird spears with side prongs. Next in order of time are the artifacts apparently belonging to the Algonquins, close relatives of the Ohio Mound Builders. There are objects of copper, flint arrowheads, perforated amulets, etc. The invasion of the Iroquois separated the Eastern Algonquins from their Ohio relatives, so that the culture of the Algonquins who lived in New England down to prehistoric times differs from that of the original stock and is influenced by contact with the Iroquois. The artifacts ascribed to them include grooved and grooveless axes, mortars and pestles, petroglyphics, pottery, bone implements, copper and metal objects, textile fabrics, etc. Besides full descriptions of the artifacts and of the location of the finds, accompanied by excellent illustrations, the author also presents some reports of early European explorers and settlers.

We Soviet Women.

By Tatiana Tchernavin. Translated by N. Alexander. E. P. Dutton and Co., New York. $2.50. 8 x 5½; 304; 1936.

This book is a collection of fifteen sketches of women encountered by the author during her life and wanderings in Soviet Russia. She is now living outside of that country and hence is able to write realistically. She lived through the Russian revolution, afterwards held official posts under the Soviets, and was imprisoned. Her husband suffered deportation to a penal settlement. Under the circumstances it is not strange that she does not like the Soviet system or philosophy. The merit of her book lies in the fact that it recounts only her own first-hand experiences and contacts. The resulting picture is a dismal one—a picture of ignorance, cruelty, stupidity, filth, official mismanagement, and something nearer to stark savagery than is likely to appeal to sensitive, cultured humanity anywhere. Civilization is a concept notoriously difficult to define precisely. But most people include somewhere in the concept some notions of the decencies and amenities of human living as significant elements. On the basis of a large and growing body of evidence this consideration plays only the smallest of rôles in the Soviet social philosophy.

Length of Life. *A Study of the Life Table. By Louis I. Dublin and Alfred J. Lotka. Ronald Press Co., New York.* $5.00. 8⅜ x 5¾; xxii + 400; 1936.

This excellent book explains very clearly what a life table is and what it tells its reader about duration of life. Life tables from antiquity to the present are compared and the great improvement in mortality at younger but not at greater ages noted. Life tables for specified causes of death are analyzed, the contributions of medical and sanitary science are discussed, and the conclusion is reached that in the light of present knowledge and without intervention of radical innovations or fantastic evolutionary change in our physiological make-up we may hope to attain a mean duration of life of seventy years. The data on the influence of geographical distribution, heredity, and occupation on longevity are presented, and the application of the life table to population and economic problems is considered. The last chapter gives a detailed explanation of King's and Jenkins' methods of life table construction. An appendix summarizes a large number of life tables for both the United States and foreign countries. This is a book that every person interested in vital statistics or public health should read.

Konstitution oder Rasse?

By Ernst Rittershaus. J. F. Lehmann, Munich. In Germany: 7.40 marks (paper); 8.80 marks (cloth). Outside Ger-

many: 5.55 marks (paper); 6.60 marks (cloth). 9 x 6; 209; 1936.

The object of this book is to examine the relationship between Kretschmer's constitutional types and the somatic habitus supposedly characteristic of different racial groups. After a prolix and ponderous discussion the author concludes that the constitutional type is, in a way, "a more primitive expression of the racial type and an indication of what the racial type will resemble." In other words, an asthenic is such because he belongs to an asthenic race. In his opinion, therefore, Kretschmer's findings on the relationship between habitus and tendency to certain forms of psychosis is not entirely correct because Kretschmer by dividing his material into asthenics and pyknics was actually studying two racial groups whose respective temperament was schizoid and cycloid. In the reviewer's opinion, the only saving feature of this work is the author's sturdy defense of the spiritual qualities of the southern German people. He himself is a southern German. It is noteworthy that in five pages of bibliography each and every publication mentioned is German.

BIBLIOGRAPHY OF CRIME AND CRIMINAL JUSTICE, 1927–1931.

Compiled by Dorothy C. Culver. H. W. Wilson Co., New York. $4.00. 10 x 6⅝; xl + 413; 1934.

This survey is international in scope and includes material published or in manuscript during 1927 to 1931 inclusive. The system of classification has been based on that used by Kuhlman in his *Guide to Material on Crime and Criminal Justice* but expansion in this field has necessitated many modifications, particularly in the sections on Police. The bibliography is divided into the following sections, each one of which has many subdivisions: Crime and criminal statistics; Offenders; Administration of criminal justice; Police; Criminal law; Criminal procedure; Judicial administration; Punishment; Probation; Institutional treatment; Pardon, parole and indeterminate sentence; and Crime prevention. While the items are entered only once, the detailed subject index makes it possible for all of them to be easily found. Annotations subjoined to items are informative and descriptive rather than critical. Included in the work is a list of periodical abbreviations and a classification outline. The volume is issued under the auspices of the Bureau of Public Administration of the University of California. It will be of great value to those whose work enters any of the fields listed.

POTLATCH AND TOTEM *and the Recollections of an Indian Agent.*

By W. M. Halliday. J. M. Dent and Sons (Canada), Toronto. $3.75. 8½ x 5½; xvi + 240 + 24 plates; 1935.

The first half of this entertaining volume is devoted to a detailed account of the custom of "potlatch" and its consequences among the Kwawkewlth (stated to be the official spelling of a name more familiar to American anthropologists as Kwakiutl) Indians of British Columbia. The essence of this idiotic institution of potlatch was for a chief to curry popularity by giving away to all and sundry vast quantities of goods, chiefly paid for by the giver with borrowed money. Its whole philosophy, both financial and social, had many other points of similarity to that of the New Deal. Potlatch nearly ruined the tribe fiscally, morally and socially. It is now rigorously prohibited by the Canadian government, with severe penalties for any chieftain who tries to start one. [Reginald, the Office Boy, suggests that we turn Kwakiutl before it is too late.]

The latter half of the book recounts some of the author's experiences during more than twenty-six years as an Indian Agent in British Columbia.

The book contains some valuable material. Unfortunately it lacks an index.

ENTRE L'ENCLUME ET LE MARTEAU (1914-1918).

By M. A. Buthine. Paul Dupont, Paris. 15 francs. 7½ x 4¾; 343; 1932 (paper).

The author is a Frenchwoman who during the last war lived in the region occupied

by the Germans. In this book she describes her conflicts with the German military authorities: the continuous exchange of insults between her and the invaders; their requisition of material useful for war purposes, foodstuffs, etc., and her attempts to hide what she could. For these activities she was, for a short time, interned in Germany, and this adventure she also relates. In brief, the book is the diary of an emotional woman in whom personal financial losses serve to augment a strong feeling of patriotism, so that every act of the invader is regarded as an insult, injustice, and so on. Even though the avowed purpose of the book is to maintain the feeling of hatred against Germany, still it succeeds in giving a clear glimpse of the economic and social disruption caused by war. The realistic reader will sympathize with the local German officials stationed among hostile people and successfully harried by such an energetic woman.

FUNDAMENTALS OF ECONOMIC GEOGRAPHY. *By Nels A. Bengston and Willem Van Royen. Prentice-Hall, New York.* $5.00. 9 x 6; xxviii + 802; 1935.

ECONOMIC GEOGRAPHY OF ASIA. *By Daniel R. Bergsmark. Prentice-Hall, New York.* $5.00. 9 x 6; xxiv + 617; 1935.

Both of these volumes have been prepared as college texts. The first is designed to furnish the subject matter for an introductory course in college geography covering a full course for one-half year, or a year's work on a three hour per week basis. The subject matter is presented in such a way as to develop a scientific and factual background for a better understanding of world production in the realms of agriculture, forestry, mining and manufacturing, and to arouse in the student of social sciences an interest in and appreciation of those influences which are molding present day conditions and activities.

The second volume is a contribution toward the understanding of the various countries of Asia, their economic-geographic regions, their major commodities, their industries and commerce. It has been the constant aim of the author properly to evaluate major occupations in the various parts of Asia, and to give a reasoned account of the economic adjustments to the environment rather than the traditional enumeration of facts.

Both of the volumes are abundantly illustrated with figures, graphs, charts and maps, and are well documented and indexed.

AFRICA DANCES. *A Book About West African Negroes. By Geoffrey Gorer. Alfred A. Knopf, New York.* $3.50. 8½ x 5¾; xv + 337 + viii + 32 plates; 1935.

This is an uncommonly interesting and informing book of travel in French West Africa, by a young Englishman who is neither a geographer nor an ethnologist in the proper academic sense of having been trained in either of these fields. In spite of this, or just possibly because of it, he manages to tell accurately and entertainingly a lot of the intimate details of negro life and living that everyone wants to know and rarely can find out from more pedantic treatises. Ostensibly his purpose in making the trip was to observe and study native dances. As it turns out the least interesting and significant parts of the book are those devoted to dancing. As Mr. Gorer plaintively says, *writing* about a dance is not much good. The same is true, of course, of music and the graphic arts. But as a document in human biology the book has real and permanent value. The illustrations are neither as numerous nor as good as they might have been. There is an excellent index.

THE MANAHOAC TRIBES IN VIRGINIA, 1608. *Smithsonian Miscellaneous Collections, Volume 94, Number 8. By David I. Bushnell, Jr. Smithsonian Institution, Washington.* 50 cents. 9½ x 6¼; iv + 56 + 21 plates; 1935 (paper).

The author describes the Indian artifacts found in what constituted Manahoac territory and which extends up the course of the Rappahannock from Fredericksburg

to Kelly's Ford and along the Rapidan from its mouth to Morton's Ford. The objects found include crudely flaked instruments side by side with celts and grooved axes and fragments of pottery with primitive characteristics. No stratified mass of camp refuse was found and so it is difficult to establish the sequence of the occupants of the place. The author arrives at the only possible conclusion, which is that this area has been continuously occupied throughout the centuries but that physical changes such as floods, etc. obscure the order of events. The author also gives a detailed description, including photographs and drawings, of the sites of discovery.

HUMAN ECOLOGY.

By J. W. Bews. Oxford University Press, New York. $5.00. $8\frac{5}{8}$ x $5\frac{1}{2}$; xii + 312; 1935.

In the author's opinion the term Human Ecology is the most appropriate to indicate the study of the relationship between man and his environment (physical, chemical, botanic, zoologic, human) and an attempt is made to synthesize what knowledge there is regarding the different forms and effects of these relationships. While the author has ably brought together the findings of many branches of science it cannot be said that his synthesis is very penetrating. What this book really contains are clear summaries of anthropogeography, psychology, anthropology, etc. but not an adequate representation or evaluation of the measure of the interrelations between man and his surroundings. The material has been obtained from standard sources and the bibliography is good.

THE FREEDOM OF MAN.

By Arthur H. Compton. Yale University Press, New Haven. $2.00. 8 x $5\frac{1}{4}$; xii + 153; 1935.

In this book, based on his Terry Foundation Lectures at Yale University, Professor Compton deals with the bearing of modern results of physics on the question of human free will. Adopting Lillie's suggestion that our deliberative processes are probably associated with neural reactions on so minute a scale as to have an appreciable uncertainty, he concludes that

> such physical laws as the conservation of energy and momentum, the initial conditions and past history, serve to define limits within which action is possible. Within these limits there may be a wide range wherein a man may do as he pleases without violating any physical law. That he actually does as he pleases is a matter of everyday experience. A man's pleasure, in other words consciousness, is thus an additional determining factor which supplements the physical laws in defining his actions.

MELANESIANS AND AUSTRALIANS AND THE PEOPLING OF AMERICA. *Smithsonian Miscellaneous Collections, Volume 94, Number 11. (Publication 3341.)*

By Aleš Hrdlička. Smithsonian Institution, U. S. National Museum, Washington. 25 cents. $9\frac{5}{8}$ x $6\frac{3}{8}$; 58; 1935 (paper).

Doctor Hrdlička traces the history of the theory that Melanesians and Australians came to the American continent in pre-Columbian days. This theory is based principally on certain skull measurements which he does not consider as adequate proof. He states that "the dolicho-stenohypsi-cephalic cranium is not extraneous but represents one of the several cranial types of both the Indian and the Eskimo; and that whatever cultural or other resemblances may appear to exist between the pre-Columbian Americas and the South Seas must have other explanations than any material accession of the peoples of the latter parts of the world to the American populations."

There is an extensive bibliography and a table of contents which serves as an index.

JOHN WHITRIDGE WILLIAMS. *Academic Aspects and Bibliography.*

By J. Morris Slemons. Johns Hopkins Press, Baltimore. $1.75. $7\frac{3}{4}$ x $5\frac{1}{4}$; xii + 109 + 1 plate; 1935.

This interesting biography of John Whitridge Williams, a man much loved and

respected around the Johns Hopkins Hospital, will make many friends among the students, patients and colleagues of the late obstetrician. The book blends within its few pages a pleasing mixture of Doctor Williams' personal traits and professional achievements and leaves the reader feeling he has had the privilege of meeting an interesting personage. A chronologically arranged bibliography of Williams' publications makes a valuable adjunct to the text.

PRIMITIVISM AND THE IDEA OF PROGRESS *in English Popular Literature of the Eighteenth Century.*

By Lois Whitney. The Johns Hopkins Press, Baltimore. $2.75. 8½ x 5½; xxi + 343; 1934.

Through most of history the belief has been common that the earliest condition of man was the best, that civilization is a corruption of the natural state of human innocence. With the development of the sciences in the seventeenth century, however, the contrary idea of the general progress of mankind began to spread. In this interesting book Miss Whitney traces the interactions of these two viewpoints, not only in the philosophers of the eighteenth century but in the didactic poets and novelists through whom their ideas reached the general reading public. Professor A. O. Lovejoy contributes a foreword.

MODERN MAN. *His Belief and Behavior.*

By Harvey Fergusson. Alfred A. Knopf, New York. $2.75. 8 x 5⅝; viii + 331 + v; 1936.

The thesis of this interesting book is that in modern civilizations there is not one system of morality but a graded series from rural communities to great cities. In the former the mores cover almost all phases of conduct, while in the latter one enjoys much wider latitude. There is a tendency to a selective adaptation of men to these different social environments: the village-born youth who can benefit by greater freedom is more likely to migrate to the city than one who feels lost without rigid external standards.

RASSEFRAGEN IN DER GEBURTSHILFE UND GYNÄKOLOGIE.

By G. Frommolt. Johann Ambrosius Barth, Leipzig. 5 marks. 9⅛ x 6¼; v + 96; 1936 (paper).

An interesting approach to the study of racial differences in fertility, age at menarche and physical factors related to child-birth. The author not only brings together in this book pertinent findings in a great mass of literature but also points out leads for further study and stresses caution in differentiating between strictly racial and environmental factors. Some interesting data are added on the incidence of tumors and carcinomas of the uterus and breast among various races.

ERINNERUNGEN UND WELTEINDRÜCKE EINES NATURFORSCHERS.

By Hans Molisch. Emil Haim und Co., Vienna. 9 marks (paper); 10.80 marks (cloth). 8¾ x 5⅞; xii + 232 + plate; 1934.

Molisch, the distinguished plant physiologist of Vienna, was born in Brünn in 1856. The son of a horticulturist, he early became interested in plants. In these pages he tells of his childhood, student days at Vienna and his teachers, his teaching and researches at Graz and Vienna, his colleagues, his two trips around the world and other travels, besides many other interesting things about himself and the persons he has met. The book is illustrated and has an "index of persons."

WAS IST VOM GEBURTENRÜCKGANG ZU HALTEN? 1, 2.

By August Lösch. Dr. August Lösch, Heidenheim (Württ.). 4.40 marks. 9 x 6; 1, 73; 2, 95; 1932 (paper).

The first edition of this work was the Helfferich prize winner in 1930. In these

two small volumes Lösch attempts to strike a comparative balance of the sum total of economic processes under the influence of different population movements. The problem is treated in an impartial, scientific manner, with the result that the conclusions and the general tone of the whole are not as pessimistic as so many treatises on this subject are apt to be. Singularly enough, the presentation is free from political bias.

AUTOBIOGRAPHY.

By Sigmund Freud. Translated by James Strachey. W. W. Norton and Co., New York. $2.00. 8 x 5½; 153 + 1 plate; 1935.

Freud's Autobiography is at one and the same time the story of his life and the history of psychoanalysis. Early in his life he was working on the anesthetic value of cocaine when a chance arose to pay a visit to his fiancée. He left the completion of his experiments to a fellow worker who finally established cocaine as a local anesthetic. Freud himself turned to the study of nervous diseases from which eventually grew his formulation of psychoanalysis. For this new edition he has added a postscript which brings the story of his life up to the present.

HEALING RITUAL. *Studies in the Technique and Tradition of the Southern Slavs.*

By P. Kemp. Faber and Faber, London. (Published in conjunction with The School of Slavonic and East European Studies, University of London.) 21 shillings net. 8¾ x 5½; xvi + 335 + 24 plates; 1935.

Healing Ritual, illustrated with numerous photographs and drawings, is a mass of information collected from the peasants in the outlying parts of the Balkans. Among other things it discusses folk psychology, healing rituals, magic, medicine and doctors, and therapy.

THE RED SPEARS OF HONAN. *A Story of Adventure in China.*

By Escott Lynn. Illustrated by J. R. Burgess. W. and R. Chambers, London and Edinburgh. 3s. 6d. net. 7⅜ x 5; 320 + 4 plates; 1935.

A blood-and-thunder tale of revolutionary China, full of bandits, looting soldiers and Bolshevik agents. Needless to say, all the Englishmen and Americans are Galahads while all the Russians are fiends in human form.

ZOÖLOGY

INSECT WONDERS OF AUSTRALIA.

By Keith C. McKeown. Angus and Robertson, Sydney. 6 shillings. 7¼ x 4¾; 252 + 16 plates; 1935.

BIRD WONDERS OF AUSTRALIA. *Second Edition.*

By Alec H. Chisholm. Angus and Robertson, Sydney. 6 shillings. 7¼ x 4¾; xiii + 299 + 33 plates; 1935.

These two additions to a series of books on the natural history of Australia should do much to stimulate popular interest in the subject. The first, by Mr. McKeown, Assistant Entomologist of the Australian Museum, recounts in an entertaining style interesting facts and occasions in the lives of the most remarkable of the Australian insects. The chapter titles alone make an irresistible appeal; for example Child slavery among ants; Ant pastoralists and dairymen; Living honey pots; The carpenter of the grass-trees; Workers in secret—the termites; The ways of crickets; The strangeness of insect courtship. The last chapter on insect foods of the aborigines is of particular interest.

No less remarkable are the Australian birds. In the preface the author says: "The idea behind this book was conceived by the publishers, who considered that Australians, and people in other countries as well, would welcome a gossipy account, and one having due respect for accuracy, of the 'Believe-it-or-Not' aspects of Australia's remarkable avifauna." With simplicity and charm he tells of the little Black-capped Honeyeater that steals human hair; of the elusive Heath Wren and its whispered mimicry of other birds' notes; of the Satin Bower-birds and their play-arbours; of the Lyre Bird revels; of

the parasitic Cuckoo that foists its eggs upon other birds; and of the many parrots and other extraordinary and beautiful birds.

Both books are rich in excellent illustrations and each has an index.

THE LOCUST OUTBREAK IN AFRICA AND WESTERN ASIA IN 1934.

By the Committee on Locust Control. Survey prepared by B. P. Uvarov. British Library of Information, 270 Madison Ave., New York. 95 cents. 9¾ x 6; 65 + 11 maps; 1935 (paper).

For the last ten years in Africa and Western Asia there has been an uninterrupted invasion of locusts. The species represented are the Desert, the Tropical Migratory, the Red and the Brown Locust. Four surveys (including the present report) have been made based on monthly reports from the various countries. The first report covered the years 1925 to 1931 inclusive. The others are for 1932, 1933, and 1934 respectively. There has been a continuous improvement in the records sent in. The most serious defect in many of the reports is that the identity of the species of locust concerned is not clearly indicated. Also frequently little or no attention is paid to the collection of records of breeding. Therefore the final surveys deal almost exclusively with the appearance and distribution of the swarms. The question is raised whether when sufficient data have been collected it may not be found that there are no periods, at least in Africa, when swarms of some species of locust are not present. If so, temporary measures could never meet the situation.

The report includes a lengthy bibliography and in a folder inside of the back cover will be found a series of maps showing swarm distributions.

SNAKE-HUNTERS' HOLIDAY. *Tropical Adventures in Search of Bats and the Bushmaster.*

By Raymond L. Ditmars and William Bridges. D. Appleton-Century Co., New York. $3.50. 8⅛ x 5⅜; ix + 309; 1935.

Around a lunch table in the New York Zoölogical Park was planned a trip to Trinidad and British Guiana to collect bats and snakes, particularly the bushmaster, of which the Zoo had had no specimen for more than twenty years. A student at the University of Michigan, Arthur M. Greenhall, and a journalist from the *New York Sun*, William Bridges, were sent ahead on a scouting expedition to round up specimens in advance of Dr. Ditmars' arrival. It was Bridges' first collecting trip to the tropics, and he writes entertainingly of the ways of naturalists and the game they seek. In a journalistic style he tells excitingly and amusingly of the search for specimens, the capture of vampire bats in dark, damp caves; expeditions at night looking for frogs and snakes; the unearthing of "the most repulsive creature in the West Indies," the giant centipede; and the fruitless search for the bushmaster. When they returned to Trinidad from British Guiana, however, they found that a bushmaster had been captured by a driller in an oil field and had been turned over to Dr. Ditmars on his arrival. This specimen was brought back to the Zoölogical Park, where it lived for only a little over two months.

Dr. Ditmars writes the first chapter on planning the expedition, and the last chapter on getting the specimens home. The rest of the book is Bridges'. There are excellent photographs and an index.

STUDIES OF GASTROPODA.

By Amadeus W. Grabau. National University of Peking, University Press, Peiping. $1.50. 9½ x 6¼; viii + 159 + 3 plates; 1935 (paper).

A group of five papers, reprints from various scientific journals. The titles are as follows: Characters of the gastropod shell; *Fulgur* and *Sycotypus*; On orthogenetic variation in Gastropoda; Value of the protoconch and early conch stages in the classification of Gastropoda; The significance of the so-called ornamental characters in the molluscan shell. In the preface the writer calls attention to the fact that little consideration up to the present time has been given to the char-

acters of immature individuals and none whatever to the protoconch. He emphasizes the fact that all the morphological features, including all the so-called shell ornamentations, have a significance which can be interpreted in terms of physiological conditions—that shell modifications are orthogenetic. The author's work is in the direction of determining (for shells of the China coast) standard individuals (morphotypes) wherever perfect material is available for the basis of comparison for each specific group and by working backwards to the Tertiary, to establish, if possible, phylogenetic series. Included in the text are 56 figures and three plates, diagrams, and a table of the genetic relationships of the species of *Fulgur* and *Sycotypus*. There is an index to genera and species.

American Bird Biographies. *Containing the Complete Life-Histories of Familiar Birds Written in Autobiographical Form.*

By Arthur A. Allen. With 10 color plates and 10 wash drawings by George M. Sutton. Comstock Publishing Co., Ithaca, N. Y. 9½ x 6½; ix + 238 + 20 plates; 1934.

This set of life histories of twenty of the more familiar of our North American birds makes a departure from the ordinary method of bird descriptions and is written in autobiographical form. Pertinent facts relating to distribution, migration, plumage, and nesting are brought out, but as each story is developed one is made keenly aware of the long and careful observations of the author on the more intimate details of bird life—differences in male and female behavior in nest building and the care of eggs and young, and many little characteristics that would pass unnoticed by the less acute observer. There are many unusual photographs among the 200 with which the book is illustrated. In addition to these photographs taken by Doctor Allen there are twenty full-page water-color portraits made by George Miksch Sutton and ten of these are beautifully done in color.

The book is concluded with a set of questions for classroom use relating to the life histories of these birds, the answers to which are to be found in the autobiographies.

Insect Enemies of Shade-Trees.

By Glenn W. Herrick. Comstock Publishing Co., Ithaca, N. Y. $5.00. 9 x 6; x + 417; 1935.

A book of the utmost importance to all those interested in the preservation of shade trees. The author, professor of economic entomology at Cornell University, through many years devoted to the study of the enemies of trees, is well fitted to write an authoritative treatise on this subject. In the first three chapters are discussed the general methods of protection from insect attack; materials and apparatus for the control of tree and shrub insects, and suggestions for the treatment of weakened trees. Then follow 26 chapters in each of which the insect enemies of an important shade tree are dealt with. The varieties of the insect pests are described, their life histories, the nature of the injuries they inflict, the means of detecting their presence and the best means of control. By a satisfactory method of cross referencing the author has avoided repetition. A final chapter is devoted to miscellaneous insect enemies of trees and shrubs. The 350 drawings and photographs form a valuable part of the book. It is well documented and contains an index of trees and shrubs as well as a general index.

Ethics of Egg-Collecting.

By Eric Parker. The Field Press, London. 5 shillings net. 8¼ x 5¼; 120 + lv; 1935.

The controversy as to whether the activities of egg-collectors resulted in the diminution of rare British birds began in 1921 when Lord Buxton brought up the subject at a meeting of the Royal Society for the Protection of Birds. In 1934 and 1935 there appeared in the *Field* a series of articles and letters on the subject, and in

this book the editor-in-chief of that journal summarizes the correspondence and clearly shows that at the present time there exists a group of egg-collectors whose activities do great harm to certain rare breeding birds. In the latter half of the book the author discusses various methods of combating the depredations of the insatiable collector "who lifts clutch after clutch from the nests of rare birds, merely for the sake of adding to the numbers of egg-shells in his possession" and considers the question "whether there are any practical steps which can be taken, not merely to enforce the law as regards the protection of rare birds, but also possibly to strengthen it," and comes to the conclusion that the existing provisions of the law are sufficient and merely lack adequate enforcement.

THE FISHES OF NEW ENGLAND. *The Salmon Family. Part 2—The Salmons. Memoir, Vol. 9, No. 1.*

By William C. Kendall. Boston Society of Natural History, Boston. $4.00 (paper); $5.00 (cloth). 12 x 9½; 166 + 11 plates; 1935 (paper).

The first part of this memoir on the Salmon Family of New England by Kendall appeared in 1914. The present memoir recognizes and defines the following New England salmonoid families on a basis of their comparative anatomy: Salmonidae, Coregonidae, Argentinidae, and Osmeridae. It deals specifically and in a thoroughly comprehensive manner with the Atlantic salmon (*Salmo salar* Linne), the lake salmon (*Salmo sebago* Girard) and the Presumpscot 'Jumper' (now extinct). Among the chapters are those on habitat, feeding habits, anadromy, life history, history of New England salmon rivers, salmon angling in New England, origin of lake salmon, sizes attained by Atlantic and lake salmon, etc., etc. Considerable historical data are given in tabular form concerning catches and markings and the recapture of marked individuals. A lengthy bibliography is included, also eleven excellent colored plates depicting both Atlantic and lake salmon in various stages of growth.

A CONTRIBUTION TO A BIBLIOGRAPHY OF THE DESCRIBED IMMATURE STAGES OF NORTH AMERICAN COLEOPTERA.

By J. S. Wade. U. S. Department of Agriculture, Washington. Free. 10½ x 8; 113; 1935 (paper).

It is at best a thankless and laborious job to prepare an extended bibliography on any subject. Once done, however, such a compilation has great value to investigators in the particular field covered by the references. Doctor Wade has assembled in the present monograph an excellent series of citations dealing with the immature stages of North American beetles. The material is arranged alphabetically according to genus and species. Each entry, where possible, refers the reader to papers dealing with the following subjects: name of genus; name of species; name of original describer of the imago; notation as to where the first and later descriptions of the immature stages occur, and, information on the "biology" or general economy of the form.

Entomologists will find this a good book to have at hand.

1001 QUESTIONS ANSWERED ABOUT YOUR AQUARIUM. *Toy Fishes—Fresh, Brackish and Salt Water. Also Your Garden Pool and Terrarium.*

By Ida M. Mellen and Robert J. Lanier. Dodd, Mead and Co., New York. $3.00.

8 x 5½; xiii + 450 + 3 color plates; 1935.

Actually this book is misnamed for instead of asking and answering 1001 questions about the aquarium it deals with 1074 and could therefore, with perfect logic, be entitled, "1074 questions answered about your aquarium." The book covers the usual topics; construction and care of the aquarium, tropical fish, gold fish, native fish, the salt-water aquarium, the question of pH, diseases of fish, the outdoor garden pool, and the terrarium. There are a number of drawings and photographs and an unusually good bibliography included in the volume. It is not a book one would care to read from cover to cover since the questionnaire method does not lend itself to such a procedure. However, aided by a com-

plete index the aquarist will find it a useful reference book for his piscatorial problems.

ECOLOGY AND LIFE HISTORY OF THE PORCUPINE (*Erethizon epixanthum*) *as Related to the Forests of Arizona and the Southwestern United States. University of Arizona Bulletin, Vol. VI, No. 5. Biological Science Bulletin No. 3.*

By Walter P. Taylor. University of Arizona, Tucson. $1.00. 9 x 6; 177; 1935 (paper).

In the forests of Arizona and other southwestern states the porcupine has been doing considerable damage to the trees. The present study has been stimulated by this fact and data have been gathered on the general ecology of the animal in the hope that the problem of control may be efficiently dealt with. The author places on record many instructive observations on the porcupine's behavior, breeding habits, food habits, enemies, etc., and the book should prove an adjunct to mammalian natural history as well as being useful to the conservationists. Some of the chapter heads, worded in an anthropocentric vein, are rather amusing, e.g., "Has the porcupine any good qualities?" and, "The porcupine an unsocial individualist," etc.

CONCERNING THE HABITS OF INSECTS.

By F. Balfour-Browne. The University Press, Cambridge; The Macmillan Co., New York. $1.50. $7\frac{3}{8}$ x $4\frac{7}{8}$; x + 169 + 9 plates; 1935.

This little book, the outcome of a course of lectures "adapted to the juvenile auditory" should be on the shelves of all school libraries. Its object is "not so much to describe the life histories of various insects as to explain how these life histories were worked out, in the hope that others may be encouraged to do similar work." The six chapters are concerned with insect collecting, the habits of bees and wasps, caterpillars, dragon flies, and water beetles, and the habits of insects and the work of man. Written simply but interestingly the book will be much read by young people and possibly by some who are not so young. It contains a number of plates and figures, a map and an index.

SERPENTS OF THE NORTHEASTERN STATES. *A Guide to the Venomous and Non-venomous Species of the North Atlantic and New England Areas. New Edition, Revised and Enlarged.*

By Raymond L. Ditmars. New York Zoölogical Society, New York. 50 cents. $9\frac{3}{8}$ x $6\frac{1}{4}$; 40 + 22 plates; 1935 (paper).

This is a simple but complete guide for the identification of the 18 non-venomous and 3 poisonous species of snakes found in the northeastern part of the United States from the Canadian border to Delaware. Following a brief chapter on the identification of snakes, is a key based upon (1) the kind of scales, (2) pattern and coloration, (3) size and (4) shape of the pupil of the eye, "which latter characteristic immediately separates the poisonous species on gross examination"; complete descriptions of the species and general range; brief but adequate sections on precautions against accidents, and the treatment of snake bites. There are 38 excellent reproductions of photographs and one color plate, and a list of eight reference books on serpents.

NOTES ON SOUTH AFRICAN WILD LIFE CONSERVATION PARKS AND RESERVES. *A Report Prepared for the American Committee for International Wild Life Protection. Special Publication No. 7.*

By Thomas Barbour and Margaret D. Porter. American Committee for International Wild Life Protection, Cambridge. $9\frac{1}{2}$ x 6; 34 + 3 plates; 1935.

At the present time a great effort is being made to preserve particular species of animals and plants rapidly becoming extinct in South Africa, and vast reserves are now being established in Rhodesia, Bechuanaland, Transvaal, Natal, Orange Free State, Basouto, South West Africa

and Cape Province. The authors of this little pamphlet visited South Africa "specifically to gather information and to carry such encouragement as we were able from the American Committee for International Wild Life Protection which has its head office here in the Harvard University Museum." They briefly describe the natural beauties and wild life of these reservations and the efforts that are being made to establish the reserves as permanent national parks. The three plates are excellent.

THE INVERTEBRATA. *A Manual for the Use of Students. Second Edition.*

By L. A. Borradaile and F. A. Potts. With Chapters by L. E. S. Eastham and J. T. Saunders. The Macmillan Co., New York. $4.00. $8\frac{1}{2}$ x $5\frac{5}{8}$; xv + 725; 1935.

This volume (reviewed in Q. R. B., 7: 483) has been revised primarily by extending the discussion on the structural and functional features exhibited by the metazoa and by adding additional material to the section on the insects. In addition, each chapter has been revised and corrected by its respective author and certain new illustrations have been prepared.

The book, in the opinion of the reviewer the best of the general invertebrate texts, should find new friends in its second edition.

CITIES OF WAX.

By Julie C. Kenly. D. Appleton-Century Co., New York. $2.50. 8 x $5\frac{1}{4}$; xv + 250; 1935.

"Cities of Wax" may well hold a prominent place among the nature books on the child's library shelf. This is a story of the life of the honey bee told in a moving, dramatic fashion that should immediately gain and hold the attention of the child. It is accurate and instructive and the text is charmingly illustrated with pen and ink sketches. There is an index.

DIE BLATT-MINEN MITTEL- UND NORD-EUROPAS. *Bestimmungs-Tabellen aller von Insekten-Larven der verschiedenen Ordnungen erzeugten Minen. Lieferung 1.*

By Martin Hering. Gustav Feller, Neubrandenburg. Subscription price for 6 numbers: (Germany and Switzerland) 12 marks; (foreign, except Switzerland) 9 marks. $9\frac{1}{4}$ x $6\frac{1}{4}$; ix–xii + 112; 1935 (paper).

This is mainly an identification list, alphabetically arranged by species of plant host, of leaf burrows made by the larval forms of Lepidoptera, Hymenoptera, Coleoptera, and Diptera. The species included are confined to those of central and northern Europe, including England. A work of interest to entomologists and botanists.

DEEP-SEA FISHES OF THE BERMUDA OCEANOGRAPHIC EXPEDITIONS. *No. 1—Family Derichthyidae. No. 2—Family Nessorhamphidae. Zoologica, Volume XX. Numbers 1 and 2.*

By William Beebe. New York Zoological Society, New York. 50 cents. $9\frac{1}{2}$ x $6\frac{1}{4}$; 51; 1935 (paper).

This paper includes a description of the systematic characters of *Derichthys serpentinus* (Family Derichthyidae) and *Nessorhamphus ingolfianus* (Family Nessorhamphidae) with some interesting remarks on the development and ecological relations of the forms studied.

THE FISHES OF UNION ISLAND, GRENADINES, BRITISH WEST INDIES, WITH THE DESCRIPTION OF A NEW SPECIES OF STAR-GAZER. *Zoologica, Vol. XIX, No. 6.*

By William Beebe and Gloria Hollister. New York Zoological Society, New York. 25 cents. $9\frac{1}{2}$ x $6\frac{1}{4}$; 16; 1935 (paper).

A faunal fish list of Union Island, one of the Grenadines, is presented with notes on each form taken at time of collection. It represents the only published list from this locality.

A Biological Reconnaissance of Navajo Mountain, Utah. *University of California Publications in Zoölogy, Volume 40, No. 14.*

By Seth B. Benson. University of California Press, Berkeley. 10¼ x 6⅝; 18; 1935 (paper).

Mutillidæ of the Philippine Islands.

By Clarence E. Mickel. Minnesota Agricultural Experiment Station, St. Paul. 10½ x 7½; 129 + 1 plate; 1934 (paper).

The Mutillid Wasps of the Islands of the Pacific Ocean (*Hymenoptera; Mutillidae*).

By Clarence E. Mickel. Minnesota Agricultural Experiment Station, St. Paul. 10¼ x 6¾; 145; 1935 (paper).

Zoologica. *Scientific Contributions of the New York Zoological Society, Volume X, Numbers, 2, 3, and 4.* Containing following papers: *Cichlid Fishes in the West Indies with Especial Reference to Haiti, Including the Description of a New Species of Cichlasoma*, by John Tee-Van; *An Annotated List of the Cyprinodont Fishes of Hispaniola, with Descriptions of Two New Species*, by George S. Myers; *Additions to the Fish Fauna of Haiti and Santo Domingo*, by William Beebe and John Tee-Van.

New York Zoological Society, Zoological Park, New York. 25 cents. 9½ x 6⅜; 38; 1935 (paper).

Nevadan Races of the Microtus Montanus Group of Meadow Mice. *University of California Publications in Zoölogy, Volume 40, No. 12.*

By E. Raymond Hall. University of California Press, Berkeley. 10¼ x 6¼; 11; 1935 (paper).

The Cycle of Trypanosoma Cruzi in Tissue Culture of Embryonic Heart Muscle. *University of California Publications in Zoölogy, Volume 41, No. 3.*

By C. A. Kofoid, F. D. Wood, and E. McNeil. University of California Press, Berkeley. 10¼ x 6¼; 2; 1935 (paper).

Differentiation in Pocket Gophers of the Thomomys Bottae Group in Northern California and Southern Oregon. *University of California Publications in Zoölogy, Volume 40, No. 11.*

By Joseph Grinnell. University of California Press, Berkeley. 10¼ x 6¼; 15; 1935 (paper).

A Distributional Study of the Peromyscus Sitkensis Group of White-footed Mice. *University of California Publications in Zoölogy, Volume 40, No. 13.*

By Ian McT. Cowan. University of California Press, Berkeley. 10¼ x 6¼; 10; 1935 (paper).

BOTANY

Pollen Grains. *Their Structure, Identification and Significance in Science and Medicine.*

By R. P. Wodehouse. McGraw-Hill Book Co., New York. $6.00. 9 x 5⅞; xv + 574; 1935.

This should be a useful book for botanists and students of hay-fever. It consists of two parts. Part I contains: historical review; methods of collecting and preparing pollen for microscopic examination; atmospheric pollen; hay-fever; pollen grain characters; and a chapter on pollen statistics by G. Erdtman. Part II is a classified list, with descriptions of morphological characters, of fossilized gymnosperms, the pollen grains of most of the wind-pollinated plants, those of the insect-pollinated species which are known or believed to contribute to the production of hay-fever, and allied forms. This is an authoritative work, but the author makes no claims as to its being the final word on the subject. To quote from the preface:

> At the present time the discovered is but a small part of the discoverable in pollen morphology. The present work, therefore, cannot be a compendium of much knowledge, if, indeed, such were desirable. Though it presents as far as possible what is known about pollen grains, it does so primarily with the object of bringing out the principles involved in their study, of showing where new discoveries may be made, and of furnishing a reliable method of approach.

The book is significantly illustrated with 14 plates and 123 figures, mostly the work of the author. It is provided with a glossary, a thirteen-page bibliography and an index.

Ethnobiological Studies in the American Southwest. *1. Uncultivated Native Plants Used as Sources of Food. The Univer-*

sity of New Mexico Bulletin, Whole Number 266. Biological Series, Vol. 4, No. 1.

By Edward F. Castetter. University of New Mexico, Albuquerque. 25 cents. 9 x 6; 62; 1935 (paper).

In a series of bulletins on Southwestern ethnobiology an attempt will be made to bring together "the results of ethnobiological researches which have been done to date in the American Southwest. An effort has been put forth to make the work *comparative*, for it is strongly believed that the ethnobiology of one Indian group compared with similar studies of other groups has a definite, far-reaching value."

While the use of native plants by various Indian tribes of the Southwest has declined since the coming of the Spaniards in 1540, nevertheless many of the groups have preserved to the present day the usage of uncultivated plants as food. The present publication, the first in the projected series, lists alphabetically by scientific name 210 native plants used by some of the Indian groups of the Southwest, particularly the Pueblo Indians of New Mexico, with an interesting discussion of the manner in which the seeds or the plants themselves are prepared for use as food, or for seasoning or coloring foods.

There is a bibliography of 45 titles and a list of the common Indian and Spanish names of the plants referred to in the text.

PRINCIPLES AND PRACTICE OF FIELD EXPERIMENTATION.

By J. Wishart and H. G. Sanders. Empire Cotton Growing Corp., London. 3 shillings. 9½ x 6; 100; 1935 (paper).

This study is divided into two parts. Part I deals with the statistical principles and methods of analysis underlying modern field experimentation. The authors have been very conservative in their recommendations of biometric methods and are careful to emphasize that caution must be used in interpretation of statistical results. Much of the statistical applications are based on R. A. Fisher's *Statistical Methods for Research Workers*, and the authors have made the fundamental concepts of that work more comprehensible as they apply to field experimentation.

Part II is concerned with the practical application of the statistical principles discussed in Part I. The authors emphasize the need of repeating experiments and of having adequate controls. Much is said about the suitable size of plots, the arrangement and shape of them and of sampling observations on plots. The survey should be very useful.

LABORATORY PLANT PHYSIOLOGY.

By Bernard S. Meyer and Donald B. Anderson. Edwards Bros., Ann Arbor, Mich. $1.75. 10¾ x 8⅜; vi + 107; 1935.

A first-rate laboratory manual such as this has long been needed by college teachers of plant physiology and the one prepared by Meyer and Anderson is far and away the best one now available. A judicious selection has been made of the standard experiments so that the whole field of chemical plant physiology has been very evenly covered. To these familiar experiments new ones have been added to demonstrate the newer additions to the knowledge of the subject. The descriptions of the procedures for performing the experiments are very well stated. Blank pages are interleaved for the student's notes. Appendices explain several of the laboratory arts in brief, including the use of the analytical balance and the microscope and set forth the formulae for the various reagents required. There is no index but there is a table of contents.

PLANT PHYSIOLOGY.

By Meirion Thomas. P. Blakiston's Son and Co., Philadelphia. $5.00 net. 8 x 5¼; xii + 494; 1935.

In the preface the author delineates the book as follows:

> The present book has been written to assist students who wish to develop the knowledge of plant physiology that they have acquired in general courses on botany given in the higher forms at school or in the first year at a university. It is therefore hoped that it will prove useful to students of chemistry, physics, agriculture, and other subjects, who have acquired such knowledge, as well as to students who are making a special study of botany.

The text is divided into the following three parts: part I, on the properties of protoplasm; part II, the absorption, translocation and elimination of water, solutes and gases, and, part III, on growth and movement. An appendix contains chapters on biochemistry and physical chemistry.

While this book cannot be considered a complete text on plant physiology, it is, nevertheless, a serious enough work to be of value to students who wish a good survey of the field.

ROCK GARDEN PLANTS.

By Clarence Elliott. Longmans, Green and Co., New York. $3.00. $7\frac{1}{4}$ x $4\frac{7}{8}$; 328 + 16 plates; 1935.

A complete list of Alpine and rock-garden plants is not given in this book, for the author has included only those with which he has had personal experience, and, as a matter of fact, not even all of those for he has frankly omitted those which bored him. However the author is a gardener and collector of wide experience, and persons who are planning to make a rock-garden or have already started one, will find much material in this book to choose from.

On the other hand, this book is more than a catalogue of plants suitable for rock-garden use. To full descriptions of the plants, alphabetically arranged by families, and cultural directions, there are added many interesting reminiscences of the author in collecting species from many parts of the world, and candid remarks about their merits and demerits.

This book should be of interest to the botanist as well as to the English gardener. American gardeners also should find the book of interest, but in following cultural directions will find it necessary to make allowance for differences of climate and temperature. The book is illustrated and indexed.

GARDEN VARIETY.

By Sir Arthur F. Hort. Longmans, Green and Co., New York. $4.20. $8\frac{1}{2}$ x $5\frac{1}{2}$; 255; 1935.

This book essentially comprises four essays: "The Winter of Content"; "A Spring Miscellany"; " 'Fantastic Summer' "; and " 'Autumn Leaves, which every Wind can Chace.' " The author was an amateur gardener and collector of plants, well-known in England. One of his chief interests was the collection of as great a number of different plants as limitations of climate and type of soil allowed. In this book he describes his garden and the plants which gave him most satisfaction in the different seasons. Much interesting material on the culture of garden plants and their history is included, but the style seems a little too pedantic for a book of this type. It has been published posthumously by Lady Hort.

WOOD HANDBOOK. *Basic Information on Wood as a Material of Construction with Data for Its Use in Design and Specification.*

By Forest Products Laboratory, Forest Research, Forest Service. U. S. Government Printing Office, Washington. 25 cents. $9\frac{1}{8}$ x 6; 325 + 6 plates; 1935 (paper).

In a practical manner this book discusses: the structure and physical properties of wood; characteristics of the more important commercial woods, their principal localities of growth in the United States, and their specific uses; strength values of various woods; grades and sizes of lumber; methods of preparing wood for various types of construction, gluing, fastening, painting and finishing; wood preservation; fire resistance of wood construction; etc. A glossary, an index, and lists of references at the end of each chapter are provided.

THE STORY OF THE PLANT KINGDOM.

By Merle C. Coulter. University of Chicago Press, Chicago. $2.50. 9 x 6; ix + 270; 1935.

This book was written for liberal arts students who are not necessarily planning to major in science. With a judicious selection of subject matter, the major facts of plant life are presented in a simple and effective way, and the student is given

a well ordered view of the various fields of botany. In tracing the evolution of the plant kingdom Coulter presents both generalized descriptions of the behavior of the members of different orders, and in several cases discussions of the life histories of specific plants—*Marchantia*, for instance. The illustrations are well selected for teaching purposes and there is an unusually complete index.

THE SPECIES OF TRADESCANTIA INDIGENOUS TO THE UNITED STATES. *Contributions from the Arnold Arboretum of Harvard University, IX.*

By Edgar Anderson and Robert E. Woodson. Arnold Arboretum, Jamaica Plain, Mass.; the authors, Missouri Botanical Gardens, St. Louis. $2.25. 10 x 7; 132 + 12 plates; 1935 (paper).

This study deals with species of *Tradescantia* found only north of Mexico. The taxonomic history, gross morphology, speciation, hybridization, and taxonomy are discussed at length.

MORPHOLOGY

REGIONAL ANATOMY. *Adapted to Dissection.*

By J. C. Hayner. William Wood and Co., Baltimore. $6.00. 9 x 6; xii + 687; 1935.

It is distinctly a novel departure to pick up a sizeable anatomy textbook and find that it contains not a single illustration. The author of this book has gone on the assumption that a real need exists for a manual of regional anatomy to supplement the usual systemic texts such as Gray's or Cunningham's. Such a manual will describe the structure of the body in terms of its topography rather than its specific anatomical and functional systems. Doctor Hayner feels that illustrations are not necessary in such a book and has consequently omitted them. Whether laboratory users will agree with him on this point remains to be seen. The book, however, is sure to be of assistance to the student in the dissecting room and to the surgeon as an aid in visualizing more completely the region of the body to be explored. The text is divided into five sections as follows: one, inferior extremity, abdomen and pelvis; two, upper extremity and thorax; three, head and neck; four, encephalon, and, five, autonomic nervous system. The B. N. A. nomenclature is used.

FASCIAE OF THE HUMAN BODY AND THEIR RELATIONS TO THE ORGANS THEY ENVELOP.

By Edward Singer. The Williams and Wilkins Co., Baltimore. $3.00. 10½ x 7¾; ix + 105; 1935.

This is a rather timely book for it fills the need, which has been growing among anatomists, for precise morphological information about the fasciae of the human body. The author points this out rather cleverly in his preface when he says,

> The dissection methods pay attention to all organs of the body and anatomical atlases bring pictures of them, but the envelops of these organs, the fasciae, are mostly left to the imagination of the student. He is able to recognize only a few fascial layers and the fasciae that he notices are in an artificially changed position giving him an inadequate basis for a proper conception. No wonder that he is inclined to consider the fasciae as opaque coverings of the organs, which should be speedily removed in order, that he may be able to expose clearly the organs in the short time at his disposal.

This book diagrams and describes with precision and clarity the various fasciae of the human body and should prove of great value to the anatomist. Since interest is developing in fasciae from the viewpoint of racial differences the physical anthropologist should also find the volume useful.

AN INTRODUCTION TO HUMAN ANATOMY.

By Clyde Marshall. W. B. Saunders Co., Philadelphia. $2.50. 7⅝ x 5; 385; 1935.

This is a brief and elementary textbook of human anatomy written "to make the student think of *Anatomy in relation to life.*" The author's interest in writing

the book can be stated in his own words as follows:

> . . . . the need became apparent for a simple textbook, written from the standpoint of an anatomist, and containing, in addition to the facts of anatomy in the narrow sense, brief accounts of the functional activities of the different organs, and of related problems of practical interest.

Despite the brevity of the book it is remarkably complete as regards general anatomical features and also has the virtue of being clearly written and well organized. Along with its many illustrations the book should prove useful to those interested in a brief, yet accurate, survey of the structure of the human body.

DEVELOPMENT OF THE PECTORAL LIMB OF NECTURUS MACULOSUS. *University of Illinois Bulletin, Vol. XXXII, No. 52. Illinois Biological Monographs, Vol. XIV, No. 1. By Hsin Kuo Chen. University of Illinois Press, Urbana.* $1.00. 10½ x 7; 71; 1935 (paper).

This monograph concerns itself with "(1) the formation of the primordial limb bud and its relations to the myotomes; (2) the differentiation of the limb bud, in which the primordia of the skeleton, musculature, and nerve plexus are laid down; and (3) the further development of the primordia which ultimately attain the conditions similar to that of the adult." The author has emphasized both the experimental embryological and the descriptive anatomical aspects of the pectoral limb and has turned out a memoir that should be useful to comparative anatomists. There are eleven plates following the text and a bibliography.

ANATOMY OF THE RAT. *Transactions of the American Philosophical Society, Vol. 27. By Eunice C. Greene. American Philosophical Society, Philadelphia.* $5.00. 11¾ x 9; xi + 370; 1935.

This excellent anatomical atlas for the albino rat is destined to become a classic. The author has been very thorough and careful in her dissections and in each of the systems she has made careful dissections of not less than ten rats. The drawings are then based on the conditions existing in the majority of cases. Man has been used as a comparison throughout the work, since it was found necessary to refer to human anatomy texts whenever doubt arose about structures found in the rat.

THE HUMAN FOOT. *Its Evolution, Physiology and Functional Disorders. By Dudley J. Morton. Columbia University Press, New York.* $3.00. 9 x 6; xiii + 244 + 9 plates; 1935.

This is an interesting and comprehensive presentation of facts about the human foot. The sections on the physiology and functional disorders give evidence to prove that foot trouble is not primarily due to weakness of the muscles and to the existence of an anterior transverse metatarsal arch. The more extensive use of X-ray in diagnosis is advocated. The book is excellently illustrated with photographs and drawings, the latter being particularly informative in the part on evolutionary development. There is a good index and a short bibliography.

THE OBSTETRIC PELVIS. *By Herbert Thoms. The Williams and Wilkins Co., Baltimore.* $2.50. 9 x 6; ix + 115; 1935.

The object of this book "is to place before practitioners of obstetrics a working knowledge of those variations and abnormalities of the bony pelvis which may affect obstetric procedure. In addition certain methods of diagnosis as carried out in the clinic with which the author is associated [Yale School of Medicine], are here set in book form for the first time."

Illustrations, an index and a bibliography have been provided.

PRACTICAL COMPARATIVE EMBRYOLOGY. *By A. Richards and A. I. Ortenburger. John S. Swift Co., St. Louis.* $1.45. 11 x 8½; 112; 1935 (paper).

This book contains the laboratory directions designed to accompany "An Outline of Comparative Embryology," already reviewed in THE QUARTERLY REVIEW OF BIOLOGY, Vol. 7, p. 242.

PHYSIOLOGY AND PATHOLOGY

A GEOGRAPHY OF DISEASE. *A Preliminary Survey of the Incidence and Distribution of Tropical and Certain Other Diseases.* *By Earl B. McKinley. The George Washington University Press, Washington.* $5.00. 10 x 6¾; xxv + 495; 1935.

This survey, incomplete as it must necessarily be at the present time, will be a valuable aid to investigators and other workers in the field of tropical medicine, besides giving an impetus to the development of this subject both by lay and professional interests. The enthusiastic cooperation which was received in its preparation indicates the recognition of the need and usefulness of such a study. It was made possible by a grant from the American Leprosy Foundation and the Division of Medical Sciences of the National Research Council. The author had as his advisers a committee composed of Doctors F. P. Gay, R. P. Strong, and the late Theobald Smith.

In the introductory chapter is reproduced the form of the entire questionnaire which was employed as a basis for collecting the information which appears in the various tables throughout the book. The division of the survey is as follows: Part I deals with the southern part of the United States and our tropical possessions; Part II, the British Empire; Part III, Asia; Part IV, the Republic of France, the Netherlands and all other countries (26 in number) not covered in the earlier sections. The statistical data are presented in tabular form, the charts or tables being supplemented with various items of factual knowledge regarding the social-economic background of each specific area. No attempt has been made to present an analysis of the data included. In Part V will be found a group of short articles (20 in number) contributed by leading authorities on certain diseases presenting world problems. Each article is followed by a summary chart which includes all the countries studied in this survey and the number of cases or deaths for each division under consideration. In an appendix is arranged scattered but valuable information from all parts of the world concerning health conditions which it was not possible to include in the main body of the report. The volume is indexed.

THE PATIENT AND THE WEATHER. *Volume I, Part 1. The Footprint of Asclepius.* *By William F. Petersen. Edwards Bros., Ann Arbor, Mich.* $3.75. 10¾ x 8¼; xx + 127; 1935.

This is Volume 1, Part 1, of the series of publications by the author on the relationship between atmospheric conditions and disease. Volumes 2 and 3 have been reviewed in this journal (Vol. 10, pp. 363–4). In this volume the first two chapters summarize the concepts of the Hippocratic school. The following chapters discuss the weather conditions of the United States, cyclonic circulation, barometric variability, etc. On the assumption that atmospheric changes produce significant alteration in the physiologic status of individuals, the author indicates three regions of the United States in which man is subjected to the greatest meteorologic variations. These regions include the New England and Middle Atlantic states, the North Central states and the Pacific states, California apparently excepted. From the statistics on causes of death, defects in drafted men, etc., the author comes to the conclusion that atmospheric conditions in these states are responsible for the comparative decreased fertility and for the higher incidence of heart disease, physical malformations, functional insanities and diseases involving disturbances of the autonomic system. On the other hand, as a group the inhabitants of these states are presumably mentally superior to those of the remaining states. The problem here investigated is very important and deserves careful study, but it must be said that the facts presented by the author

do not demonstrate the validity of his conclusions. The statistical analysis is particularly faulty. The fact that in some states there is a higher incidence of certain diseases than in some other states does not mean that there exists correlation between atmospheric conditions and disease unless it can be shown that, *caeteris paribus*, there is direct association between variation in atmospheric condition and in disease incidence. This the author has failed to do.

THE EFFECTS OF CEREBELLAR LESIONS UPON THE HABITUATION OF POST-ROTATIONAL NYSTAGMUS. *Comparative Psychology Monographs, Vol. 12, No. 1, Serial No. 56.*

By Ward Halstead. Johns Hopkins Press, Baltimore. $1.75. 10 x 6⅞; 130; 1935 (paper).

It has been shown that repeated elicitation causes a decrease in the duration of post-rotational nystagmus. A number of hypotheses have been advanced to explain this "habituation" phenomenon and here the author reports his investigation regarding the effect on pigeons of lesions of the anterior and middle lobes of the cerebellum. Three types of experiments were conducted. The first was to determine whether birds with an experimental cerebellar lesion would habituate as readily as unoperated birds. It was found that at the first trial the post-rotational nystagmus was about equal for both unoperated and operated birds. However, for the latter the habituation effect was markedly and significantly less. The second and third sets of experiments were conducted to ascertain whether a cerebellar lesion influenced birds who had already been habituated. It was found that the operated birds showed a marked loss of the habituation effect while the control group did not. It is noteworthy that a significant degree of habituation persisted in both operated and unoperated birds for as long as three months after the habituation period. The author believes that the habituation effect is of the nature of a "learning process" and therefore from the facts observed concludes that the cerebellum participates directly in learning situations and may play a dominant part in certain types of "higher" activities. While these ingenious experiments have been well conducted and controlled, it does not seem that this conclusion is warranted without further knowledge regarding the actual mechanism which produces nystagmus and the precise anatomic and physiologic relations between the vestibular apparatus and the cerebrum and cerebellum.

SCENERY AND THE SENSE OF SIGHT.

By Vaughan Cornish. The Macmillan Co., New York; The University Press, Cambridge. $3.00. 8⅜ x 5½; xii + 111 + 10 plates; 1935.

During his travels for many years in England and on the continent the author, from observations of many natural scenic phenomena, came to the conclusion that scenic effects are dependent upon unconscious eye habits. The sun, for example, looks enlarged when it sets because we unconsciously reduce the field of vision. " . . . the more the eye takes in vertically the more it takes in horizontally and the less impressive are both dimensions. If one may speak of the eye as an organ possessed of personality I should describe this personality as of the kind that can only attend to one theme at a time but has great power of appreciating variations of the theme. By a theme I mean in this connection a visual category, and the categories with which I am dealing . . . are height, breadth, distance and area."

There are many other phenomena described and analyzed with a great deal of talk about angles and arcs which at times is only confusing because the author often omits to say just what he is measuring. There are several free hand impressionistic drawings.

THE CEREBROSPINAL FLUID AND ITS RELATION TO THE BLOOD. *A Physiological and Clinical Study.*

By Solomon Katzenelbogen. Johns Hopkins Press, Baltimore. $5.00. 9 x 6; xix + 468; 1935.

This book grew out of an attempt of the author to determine the exact status of our knowledge about the cerebrospinal fluid. Since so much that is contradictory has been published the author felt that it was high time to set down in an organized manner the available data, and to review and analyze it critically.

The book falls into two parts. Part I is chiefly concerned with the origin, mode of formation and circulation of the cerebrospinal fluid. The second part of the book deals with the "physico-chemical constitution of the cerebrospinal fluid, as compared to that of blood in physiological and pathological conditions. In this part the rôle and composition of the cerebrospinal fluid and certain therapeutic procedures are discussed in the light of the present day concept of the function of the barrier between blood and cerebrospinal fluid."

The author is careful to discuss all theories pro and con and in the light of his own research work in physiology and neurology. The book will make an excellent reference source.

SENSATION: ITS MECHANISMS AND DISTURBANCES. *An Investigation of the Most Recent Advances. The Proceedings of the Association, New York, December 27th and 28th, 1934.*

By Association for Research in Nervous and Mental Disease. Editorial Board: Clarence A. Patten, Angus M. Frantz, Clarence C. Hare. Williams and Wilkins Co., Baltimore. $7.50. 9 x 6; xxiii + 541; 1935.

This volume reports the Proceedings of the 1934 meeting of the Association for Research in Nervous and Mental Disease. The program of this meeting consisted of a symposium on the neuropathology of sensation. The papers that were presented have been arranged into four sections. In the first are those which discuss peripheral nerves and sensory nerve endings. The second section contains articles on visceral sensations. Articles concerning sensory tracts and mechanisms in the cord and brain are found in the third part. In the last section are the clinical reports on several forms of sensory disturbances. The majority of articles describe the results of original investigations and in general all contain a fairly complete survey of the literature on the subject.

HOW TO LIVE FOR A HUNDRED YEARS AND AVOID DISEASE.

A Treatise by Luigi Cornaro, the Sixteenth Century Italian Centenarian. Translated by George Herbert, with an Introduction by George Cooke. The Alden Press, Oxford. 2s. 6d. net. $7\frac{3}{8}$ x 5; 63; 1935.

Luigi Cornaro lived to be a hundred years old and in his well-known pamphlet attributed his longevity to a restricted diet: a daily ration of 12 ounces of food, consisting of broth, eggs, bread and meat, and 14 ounces of wine. This booklet presents a translation of that pamphlet in addition to an introduction equal to it in length and written by a Mr. George Cooke. This gentleman has a rather low opinion of the diets advocated by medical dietitians and proceeds to say so in a direct fashion. At the same time he demonstrates a rather limited knowledge of the processes of metabolism. It is noteworthy that neither this book nor others of the same kind ever advance one good reason why anyone should want to attain old age at the sacrifice of our one *raison d'être*, satisfaction of physical and spiritual desires.

A TEXTBOOK OF PHYSIOLOGY. *Fifth Edition.*

By William D. Zoethout. C. V. Mosby Co., St. Louis. $4.00. 9 x 6; 694; 1935.

The fifth edition of this textbook of physiology for dental and pharmacy students has been altered from previous editions (reviewed in Q. R. B., vol. 4, p. 286) by rewriting most of the text and revising and bringing up to date the chapters on hormones, vitamines, muscle physiology and the nervous system.

Many new illustrations, a glossary of commonly used terms, and a list of prefixes and suffixes have been added. Certain supplementary and advanced material has been condensed and set in small type. The book is readable, authoritative, and should continue to be useful for the group it has been serving.

DIE ORGANISCHEN UND FUNKTIONELLEN ERBKRANKHEITEN DES NERVENSYSTEMS.

By Friedrich Curtius. Ferdinand Enke, Stuttgart. 13 marks (paper); 14.80 marks (cloth). 10 x 6½; vii + 195; 1935.

The first part of this book, comprising about one-third of the whole, is devoted to a general discussion of the inheritance of diseases of the nervous system and the variability in their manifestation among members of the same family. In the second part each disease is discussed separately with as much information as is at present known concerning the frequency of occurrence, racial and general pathology, anatomy, symptomatology, mode of inheritance, and diagnosis. These diseases are classified as follows by system or type: pyramidal system, spinocerebellar system, extrapyramidal system, diffuse, developmental disturbances, nystagmus and atrophy of the optic nerve, and functional diseases.

Author and subject indices are provided. This is an important book for both students of nervous disease and heredity.

HEMISPHERIC CEREBRAL DOMINANCE AND HEMISPHERIC EQUIPOTENTIALITY. *Comparative Psychology Monographs, Vol. 11, No. 5, Serial No. 55.*

By Samuel A. Kirk. Johns Hopkins Press, Baltimore. 75 cents. 10 x 7; 41; 1935 (paper).

Paucity of experimental evidence in support of the opposing theories of hemisphere cerebral dominance and hemisphere equipotentiality in the regulation of certain types of behavior gave rise to the investigation reported in this monograph. The results indicate that in the case of the rat: (1) hand preference is changed following cortical destruction within a critical area of the anterior portion of the contralateral hemisphere; (2) the hemispheres appear to be equipotential for visual function; and (3) there is no support for the theory of cerebral dominance as applied to intelligent behavior as determined by Maier's reasoning test.

THE MEDICAL VOODOO.

By Annie R. Hale. Gotham House, New York. $2.50. 8¼ x 5½; 338; 1935.

This is a frontal attack on vaccination, antitoxins, serum therapy, and the science of immunology generally. It is stylistically more entertaining and more shrewdly put together than the writings of most anti-vaccinationists, but from the viewpoint of logic it is the same old eye-wash. As Augustus de Morgan pointed out long ago the tribe of paradoxers never really changes; they only alter their box of tricks. Mrs. Hale is obviously a sincere person, who honestly believes that vaccination and immunization against diphtheria are nonsense or worse, but so the perpetual motion addict, or the circle squarer, sincerely believes he is right and all the mathematicians are wrong. Nothing can be done about it. But it really does not matter much, because the world and mankind march on regardless of the paradoxers.

RAPPORT SUR LE PÈLERINAGE AU HEDJAZ *de l'Année de l'Hégire 1353 (A.D. 1935).*

Conseil Sanitaire Maritime et Quarantenaire d'Egypte, Alexandria. Free. 12½ x 9; 113 + 6 plates + folding map and 5 folding tables; 1935 (paper).

This is the report of the health conditions of the Mohammedans who in 1935 made the pilgrimage to Mecca. Compared to 1934, the number of pilgrims this year has increased from 50,000 to 80,000. Thanks to the public health regulations,

which are being enforced with great vigor by the authorities of all countries concerned, such an agglomeration of people has not produced the characteristic epidemics of the past. This report presents data on the number of caravan ships passing the Suez Canal, the number of pilgrims carried, the results of medical and bacteriologic examinations at quarantine ports, the country of origin of these pilgrims and the particular health regulations of each country.

CLASSICAL CONTRIBUTIONS TO OBSTETRICS AND GYNECOLOGY.

By Herbert Thoms. Charles C Thomas, Springfield, Ill. $4.00. 9 x 5⅝; xxiii + 265 + 1 plate; 1935.

In this book are presented in English fifty-nine selections from the works of eminent contributors and discoverers in obstetric and gynecological practice, from early times up to 1900. The material is grouped under several headings: general obstetrics; the course of labor; the pathology of pregnancy; the operations of obstetrics; puerperal infection; deformities of the pelvis; and gynecology. Brief historical and biographical comments precede most of the selections. Portraits and facsimiles of title pages and text pages of famous works form an interesting feature. The book will be of interest to physicians and students of medical history.

TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Tome X. Physiologie Nerveuse. (Deuxième Partie), Fascicules 1 and 2. By F. Bremer, R. Caussé, A. et B. Chauchard, J. Froment, R. Garcin, L. Garrelon, J. Haguenau, A. Hautant, A. Le Grand, F. Lemaitre, J.-B. Logre, L. Merklen, G. Milian, N. Peron, H. Péron, D. Santenoise, A. Strohl, E. Velter, M. Vidacovitch. Published under the direction of G.-H. Roger and Léon Binet. Masson et Cie, Paris.* 220 francs (paper); 250 francs (cloth), for two volumes. 9⅝ x 6⅝; xv + 1579; 1935.

This is the tenth volume of a series on human physiology, the previous volumes of which have already been reviewed in this journal. As with the other volumes in this series there are the same defects which arise from the fact that many specialists have contributed to the work. This volume deals principally with the central nervous system. There is an introductory chapter on psycho-physiology, followed by chapters on the physiology of the brain, the cerebrospinal fluid, the cranial nerves, sympathetic and parasympathetic nervous system, the skin, the cutaneous sensory system, languages, auditory, visual, taste and odor.

A B C OF THE ENDOCRINES.

By Jennie Gregory. Williams & Wilkins Co., Baltimore. $3.00. 11½ x 9; xiii + 126; 1935.

This represents an attempt to bring the scientifically determined facts of endocrinology before the layman in a pictorial form that is easily understood. There is no new or original work reported in this book, though there is recent information that has not yet been put in the more elementary books. The book is simple, well thought out, and should help the layman to understand a great deal better all this talk about "glands".

QUARTERLY BULLETIN OF THE HEALTH ORGANISATION, LEAGUE OF NATIONS, *Vol. 4, No. 3.*

World Peace Foundation, Boston and New York. 65 cents. 9½ x 6¼; 144; 1935 (paper).

BIOCHEMISTRY

HVALRÅDETS SKRIFTER. *Scientific Results of Marine Biological Research. Nr. 11. Contributions to the Study of Whale Oils. Chemical Analysis of Samples of Blue Whale Oils, by I. Tveraaen; Studies in the Biochemistry of Whale Oils, by Alf Klem.*

Edited by Universitetets Biologiske Labora-

torium. Jacob Dybwad, Oslo. 10¾ x 7; 108; 1935 (paper).

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Both papers are equipped with a bibliography.

VITAMINS *in Theory and Practice.*

By Leslie J. Harris. The University Press, Cambridge; The Macmillan Co., New York. $3.00. 8 x 6; xix + 240 + plate; 1935.

This book is based on four lectures given at the Royal Institution, London, in 1934. The history of vitamin discovery and research is a romantic subject and the author has managed to write a thoroughly readable and enjoyable treatise without departing from actual scientific or historical facts. The vitamins are discussed in the order in which they were first studied: Beri-beri and vitamin B_1; Pellagra and vitamin B_2; Scurvy and vitamin C; Vitamin D and rickets; Vitamin A; Vitamin E, diet and sterility. The last chapter is a discussion of what to eat, and as is often the case in such discussions one gathers there is nothing like milk. But there is much sound advice particularly for those families who must be fed on reduced budgets.

THE BIOCHEMISTRY OF THE LIPIDS.

By Henry B. Bull. Burgess Publishing Co., Minneapolis. $3.25. 11 x 8½; v + 127; 1935.

This monograph on the biochemistry of the lipids is divided into two parts. Part I deals with the chemistry of the fatty acids, soaps, alcohols, hydrocarbons, sterols, fats and oils, phospho-lipids and glyco-lipids. Part II is concerned chiefly with the physiology of the lipids and their rôle in plant and animal life. The intention of the author is to collect and organize all the most recent work on the lipids into a text for students, rather than to report on original research. This monograph should be very useful.

INFLUENCE OF LIGHT ON SOME BIOCHEMICAL PROCESSES.

By N. R. Dhar. Society of Biological Chemists, Indian Institute of Science, Hebbal P. O., Bangalore. Re. 1. 8½ x 5½; 73; 1935 (paper).

An attempt to show that sunlight is beneficial to soil, and plant processes. The author points out from the results of experimentation that both the ammonification and nitrification in soil are remarkably increased by heat and sunlight and that both processes may go on in the presence of sunlight even if there are no bacteria.

TRAITÉ DE CHIMIE ORGANIQUE. *Tome III. Hydrocarbures Aliphatiques Saturés et Non Saturés. Longues Chaînes Cycliques. Cyclanes, Cyclènes et Terpènes Monocycliques. Dérivés Halogénés, Nitrosés ou Nitrés des Hydrocarbures Précédents. Industries Dérivées de l'Acétylène. Dérivés Chlorés Industriels.*

By J. Doeuvre, G. Dupont, V. Grignard, R. Lespieau, J. Lichtenberger, L. Palfray, L. Ruzicka, F. Swats. Published under the direction of V. Grignard and Paul Baud. Masson et Cie, Paris. 150 francs (paper); 170 francs (cloth); 10 x 6½; xix + 784; 1935.

The scope of this, the third, volume of a

comprehensive series which will ultimately comprise fifteen volumes, is sufficiently indicated by the subtitles. Volume 1 was noticed in the immediately preceding number of this REVIEW, and volume 2 has not yet been published.

BIOCHEMICAL AND ALLIED RESEARCH IN INDIA IN 1934.

Society of Biological Chemists, Indian Institute of Science, Bangalore. Subscription price Rs. 2 per year. 8½ x 5½; 107; 1935 (paper).

SEX

LA CASTRATION CHEZ L'HOMME *et les Modifications Morphologiques qu'elle Entraine. Recherches sur les Adeptes d'une Secte d'Eunuques Mystiques, Les Skoptzy.* *By Eugène Pittard. Masson et Cie, Paris.* 60 francs. 9¾ x 6½; 329; 1934 (paper).

Skoptzy is the name given to a mystic sect found in Russia and Roumania and estimated, in 1871, to number more than 16,000. Its fundamental and distinctive tenet is that "life eternal" can be obtained only by castration. In the males, this is carried out by simply severing the penis and testicles; in the females, by mutilation of the breasts and vagina. Persecution by both the Russian and Roumanian police has not been very effective and it appears that this sect does not lack proselytes. These comprise children obtained in several ways and adults converted either by emotional or economic means.

It is evident that the Skoptzies are an interesting material for study by the physician, anthropologist and human biologist. However they are a suspicious people and very little knowledge about them has been obtained. This contribution by the author is therefore invaluable. He was able to acquire the confidence of some Roumanian Skoptzies and at different periods collected a series of anthropometric measurements on some 50 male adults who presumably had been castrated before puberty (hairless) and on an equal number who had been castrated after puberty (hairy). The essential findings may be summarized as follows. The hairless Skoptzies are markedly taller than the hairy Skoptzies and the Roumanians in general. In fact, as a group, they are even taller than the Sara negroes. Their superior height is due to an excessive leg length. The head length, breadth and height of the hairless Skoptzies are markedly inferior to those of the other Skoptzies and of the general Roumanian population. This is true also for those indices which present the above head dimensions as percentages of stature. All the other characteristics usually found associated with eunuchism are also observed by the author in the hairless Skoptzies. The hairy Skoptzies, on the average, present no characteristic somatic changes, when compared to the general population, except for some over-development of breasts and buttocks and signs of precocious senility.

SEX IN HUMAN RELATIONSHIPS.

By Magnus Hirschfeld. John Lane, The Bodley Head, London. 8s. 6d. net. 8½ x 5½; xxii + 218; 1935.

Dr. Hirschfeld, recently deceased, was one of the leading investigators in sexology. In this book, of a theoretical and philosophical nature, he summarizes his views on normal and abnormal sexual behavior and illustrates his method of study of the different aspects of the problem. It is interesting to cite his definition of love: "Love is a conflict between reflexes and reflections"; to which he adds: "For every individual, love is determined by the interactions of his psycho-glandular constitution." From this viewpoint the author discusses the interplay between mental attitudes and physiologic reactions in the game called love. The questionnaire submitted to his patients and which he reports has been so prepared as to permit the author to integrate the subject's sex life with his biologic constitution. The book includes chapters on the attraction between similars and dissimilars, fetishism and a critical summary of Freud's theories. Not very well translated, this book appears superficial

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and vague in a number of points. However, within its scope, it is satisfactory and the reader will enjoy the author's show of erudition.

TOWARDS SEX FREEDOM.

By Irene Clephane. John Lane, The Bodley Head, London. 8s. 6d. net. 8½ x 5½; ix + 243; 1935.

An interesting story of the progress of woman during the last hundred years showing the growth in her education and the improvement in her economic position. Beginning with a sketch of Mary Wollstonecraft and her times, the author goes on to describe the place women occupied in the reign of Queen Victoria. She writes of the Contagious Diseases Acts, of child prostitution, of the development of birth control, and of the effect of the World War upon woman by the upheaval of many of the prevailing conventions.

SEX RECOGNITION IN THE GUPPY LEBISTES RETICULATUS PETERS. *Zoologica. Scientific Contributions of the New York Zoological Society, Vol. XIX, Number 5.*

By C. M. Breder, Jr., and C. W. Coates. New York Zoological Society, Zoological Park, New York. 20 cents. 9½ x 6⅜; 20; 1935 (paper).

After a series of experiments the authors conclude that sex recognition in the male guppy is feeble and entirely visual, as "any object of appropriate size will stimulate the mating instinct if showing the characteristic motions of a living fish." The female is indifferent to sex activity but fertilization is insured by the aggregating behavior of the species and the great activity of the males. Tables, graphs, and a short bibliography are given.

SEX BEHAVIOR IN MARRIAGE.

By Charles A. Clinton. Pioneer Publishing Co., New York. $2.00. 7½ x 5; 159; 1935.

This book is written for the layman and abounds in sentimentality. It contributes nothing new and is limited in all directions by the moral point of view of the author, who is more interested in asserting that love is a beautiful thing than in discussing it from a technical point of view.

BIOMETRY

THE GROWTH OF THE SURFACE AREA OF THE HUMAN BODY.

By Edith Boyd. University of Minnesota Press, Minneapolis. $5.00. 10 x 6⅞; xi + 145; 1935.

This monograph is an important contribution to the subject of measurement of the surface area of the body. The author outlines in a thorough and critical manner the different methods of obtaining the values of this dimension either by direct measurements or by estimations. She has abstracted from the literature 231 measurements and attempts to find an adequate mathematical expression of the age variation in the relationships between surface area and weight and weight and height. The results are not satisfactory as the author herself notes. Especially interesting is the graphic representation of the rate of growth of the body surface area. It takes the form of two asymmetrical sigmoid curves. The point of inflection for the first curve is at birth, for the second it is at puberty. To this reviewer it seems that in this case, as well as for a few others, the data permitted a finer biometric analysis. This is the only criticism, if it may be so regarded, of a noteworthy and useful study.

ELEMENTS OF STATISTICS. *With Applications to Economic Data.*

By Harold T. Davis and W. F. C. Nelson. The Principia Press, Bloomington, Ind. $4.00. 9¾ x 6¾; xi + 424; 1935.

As the title implies this excellent textbook was written primarily for the statistical training of students of the social sciences. The relation of statistics to economics is

therefore developed and the problems are drawn from economic sources. Algebraic processes are given in full and the proofs do not presuppose a knowledge of calculus. The appendices give bibliographical notes on early mathematical economists, explanations of logarithms and the use of tables, and tables of logarithms, exponential functions, squares, square roots, reciprocals, ordinates and areas of the probability function, goodness of fit and coefficients for fitting straight lines and parabolas.

AN INTRODUCTION TO THE THEORY OF FUNCTIONS OF A COMPLEX VARIABLE.

By E. T. Copson. Oxford University Press New York. $8.50. $8\frac{1}{4}$ x 6; iv + 443; 1935.

This textbook deals with complex numbers, the convergence of infinite series, functions of a complex variable, Cauchy's theorem, uniform convergence, the calculus of residues, integral functions, conformal representation, the gamma and hypergeometric functions, Legendre and Bessel functions, the elliptic functions of Weierstrass and Jacobi, elliptic modular functions and Picard's theorem. References and exercises are given at the end of each chapter.

EINFÜHRUNG IN DIE VARIATIONS- UND ERBLICHKEITS-STATISTIK.

By Erna Weber. J. F. Lehmann, Munich. In Germany: 9.60 marks (paper); 11 marks (cloth). Outside Germany: 7.20 marks (paper); 8.25 marks (cloth). $8\frac{7}{8}$ x $6\frac{1}{8}$; 255; 1935.

This book is written for the statistical training of anthropologists, geneticists, and students of constitution. Besides the usual exposition of centering constants, variability, correlation, and probability, methods for determining the applicability of genetic hypotheses from human pedigrees are dealt with. Professor F. Lenz contributes a foreword.

MATHEMATICAL TREATMENT OF THE RESULTS OF AGRICULTURAL AND OTHER EXPERIMENTS.

By M. J. van Uven. P. Noordhoff, Groningen. 9.50 florins (paper); 10.50 florins (cloth). $9\frac{3}{4}$ x $6\frac{3}{4}$; vi + 309 + folding chart; 1935.

This is essentially a textbook of least squares and analysis of variance. Where the calculus is used in the proofs an alternative proof, involving only elementary mathematics, is also given. A useful feature is a brief glossary of statistical terms in English, Dutch, German, Danish, Swedish, French, Italian, Spanish and Esperanto.

CONTINUOUS INVESTIGATION INTO THE MORTALITY OF ASSURED LIVES. *Monetary Tables A 1924–29. Vol. I. Vol. II. Vol. III (Joint Lives).*

Published on behalf of The Institute of Actuaries and The Faculty of Actuaries in Scotland. University Press, Cambridge; The Macmillan Co., New York. Vol. I, $22.50; Vol. II, $17.50; Vol. III, $11.00. $9\frac{3}{4}$ x 6; Vol. I, xxxix + 339; Vol. II, x + 225; Vol. III, x + 99; 1934–35.

These volumes give mortality functions and monetary tables based on the combined experience of a number of British and a few Canadian and Australian life insurance companies. The original data from which these tables are derived were noticed in Volume 9, page 489, of this REVIEW.

PSYCHOLOGY AND BEHAVIOR

GHOSTS I HAVE TALKED WITH.

By Henry C. McComas. The Williams & Wilkins Co., Baltimore. $2.00. 8 x $5\frac{1}{8}$; viii + 192; 1935.

In 1925 the American Society for Psychical Research decided to employ an experimental psychologist, trained in the methods of the psychological laboratory, to investigate the phenomena in which they were interested. This entertaining book narrates Dr. McComas's experiences in this position. Perhaps the most amus-

ing part of the book is the account of his tests of the celebrated Margery (Mrs. Crandon). Although the conditions imposed by Dr. Crandon made any crucial test impossible, Dr. McComas determined to go ahead with the investigation. However, at the end of one of the séances someone suggested that a thorough examination of Margery and her cabinet be made. "Mrs. Crandon coughed, gagged, leaned over as though suffering from violent *mal de mer*. Then aided by the stenographer she hurried to the bathroom and we could hear a very good imitation of a passenger crossing the English Channel. Dr. Crandon left the room to see his wife. We took a flashlight and examined the floor as we felt that Psyche had been firing blank cartridges. She had."

After this episode Dr. Crandon refused to allow any further investigation. Following nearly a year of fruitless negotiation Dr. McComas arranged a séance of his own in which he reproduced a number of the Margery phenomena, including the ringing of the bell-box, whistling and whispering by the medium using a voice cut-out of the type used by Margery, reading cards in the dark and the appearance of psychic lights. So impressed were the sitters that fifteen of them voluntarily signed a statement that these phenomena were done by no normal means known to them. Five of them, who had been present at Margery's séances, agreed that Dr. McComas's phenomena were quite as good as hers.

Shortly after the séance I wrote to the people who had participated and told them that the Hindoo and I had worked up these effects in order to show Dr. Crandon that what Margery did could be done by natural means and that Dr. Crandon should permit an investigation much more thorough-going than any that he had allowed up to date. Some of my sitters took it all in good part, others were somewhat indignant.

COMPARATIVE PSYCHOLOGY: *A Comprehensive Treatise. Volume I. Principles and Methods.*

By Carl J. Warden, Thomas N. Jenkins, and Lucien H. Warner. The Ronald Press, New York. $4.50. $8\frac{5}{8}$ x $5\frac{5}{8}$; x + 506; 1935.

This is the first of three volumes under the general title of "Comparative Psychology" and deals with Principles and Methods. The other two volumes will cover Plants and Invertebrates, and Vertebrates.

The aim of the present book is to prepare the student in the background and the fundamentals of methodology so that the later two volumes may be more readily comprehended. The first four chapters give a broad historical and theoretical introduction to the problems of comparative psychology. The next two chapters "Methods of Testing Receptive Capacities" and "Methods of Testing Reactive Capacities" are an attempt to demonstrate in a critical manner the methodology of the science. The final chapter "Comparative Morphology and Physiology of Organisms" deals in a summary fashion with the structure and function of the receptive, transmissive and reactive mechanisms of living organisms.

The work is thoroughly documented and there are nearly a hundred pages of bibliography for the seven chapters. It should be an invaluable reference for the research worker as well as an excellent text.

PRINCIPLES OF ANIMAL PSYCHOLOGY.

By N. R. F. Maier and T. C. Schneirla. McGraw-Hill Book Co., New York. $4.00. 9 x $5\frac{7}{8}$; xiii + 529; 1935.

The authors describe in the preface the scope and purpose of their book as follows:

This work is designed to serve as a systematic textbook of animal behavior for courses in psychology and biology. Part I covers the behavior of animals below the mammals, a comparative treatment in which we have endeavored not only to characterize each important animal type but also to work out certain fundamental principles of animal adjustment. In Parts II and III these principles are developed further as the major problems of animal psychology are attacked in connection with the behavior of mammals.

It can be fairly said that the text lives up to the designs held for it by the authors. It should prove a very useful book indeed to the general psychologist. One of the important contributions of the book is that it helps to synthesize and assemble

much experimental work which has hitherto existed only in various isolated papers. Each chapter, as well as the entire volume, is followed by a helpful bibliography.

DÉTERMINISME ET VARIABILITÉ DANS LE COMPORTEMENT DES ORGANISMES. *Actualités Scientifiques et Industrielles, 261. Exposés de Biométrie et de Statistique Biologique, VII. By W. J. Crozier. Hermann et Cie, Paris.* 15 francs. 10 x 6½; 57; 1935 (paper).

In this interesting monograph Professor Crozier shows that when rats run up an inclined plane their mean direction may be fitted with a mathematical function of the angle of inclination of the plane which is capable of a physiological interpretation. The parameters of the function differ from one strain of rats to another, while in crosses they behave as Mendelian characters. The variation is also a function of the intensity of the exciting force. He concludes therefore that the conditions of mechanistic determinism are fulfilled.

ROOTS OF CRIME. *Psychoanalytic Studies. By Franz Alexander and William Healy. Alfred A. Knopf, New York.* $3.00. 8 x 5¼; viii + 305 + iv; 1935.

A psychoanalytic study of eleven criminal males and females. Beginning with their case histories the authors write fully about each character and carry you through each analysis step by step, often recording in the patients' own words their ideas and dreams, and the analyst's interpretation of them. Most of the analyses were begun in prison and many were continued after the patient's release.

THE FUNCTIONS OF THE VISUAL AREAS OF THE CEREBRAL CORTEX OF THE RAT IN THE LEARNING AND RETENTION OF THE MAZE. II. *Comparative Psychology Monographs, Vol. 12, No. 2, Serial No. 57. By Yü-Chüan Tsang. The Johns Hopkins Press, Baltimore.* 75 cents. 10 x 6⅞; 41; 1936 (paper).

The first part of this study was reviewed in THE QUARTERLY REVIEW OF BIOLOGY, Volume 10, p. 373. This paper is a report of further investigations along the same line. The experiments indicate that there is a non-visual function of the visual cortex, although its exact nature has not yet been determined.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

OUTPOSTS OF SCIENCE. *Journey to the Workshops of Our Leading Men of Research. By Bernard Jaffe. Simon and Schuster, New York.* $3.75. 9¼ x 6; xxvi + 547; 1935.

The writing of a first rate book on semi-popularized science is a difficult task. To do a good job the author must combine accuracy of statement without sacrifice of interesting reading. Consequently, many such books fail to meet the standards set by the experts, the reading public or both. The present volume should prove an exception however, for it is, by and large, both interesting and authoritative. Doctor Jaffe has selected his topics and personalities with care and has developed his thoughts and opinions realistically and with a minimum of exaggeration.

The book is divided into two parts: part I, dealing with the biological topics and part II, with physical topics. In the biology section the author stresses the work of Morgan in genetics, Hrdlička in anthropology, Welch in pathology, Slye in cancer, Abel in endocrinology and pharmacology, Meyer in psychobiology, McCollum in nutrition, and Howard in entomology. Each of these discussions attempts to point out the major principles of the several fields and to evaluate the contributions of the various personalities in their respective niches. The reviewer found all of the chapters interesting and had no quarrel with the approach except in the chapter on entomology where Doctor Jaffe spends the entire time discussing the economic field of insect control and eradication. Interesting and important

as this subject is it seems a pity that more data on theoretical entomology were not included.

On the whole, this is an excellent volume and should be read and enjoyed by professional and lay persons alike. Page-sized portraits of most of the scientists discussed make an interesting addition to the text.

ARISTOTLE'S CRITICISM OF PRESOCRATIC PHILOSOPHY.

By Harold Cherniss. The Johns Hopkins Press, Baltimore. $4.00. 9 x 5⅞; xvi + 418; 1935.

A sound, thorough, and scholarly treatise, of great value to serious students of the history of science. Its purpose is in general to examine objectively, and apart from what later commentators said about them, the views of Aristotle's predecessors. This is done with great thoroughness, meticulous documentation, and penetrating scholarship. The author justifiably hopes that the investigation should lead to a better comprehension of Aristotle's own philosophical method,

> for once the reports and critiques have been returned to their proper contexts and their relationship to those contexts analyzed, Aristotle's own conception of the unity of his work both in itself and as the culmination of all previous thought assumes a new significance. In the light of this relationship, too, it may appear that the proper approach to Aristotle's systematic philosophy is that which corresponds with his own notion of the origin of his system, namely by way of his predecessors both in their true historical form and in their metamorphosis as lisping Aristotelians.

THE ATTITUDE OF VOLTAIRE TO MAGIC AND THE SCIENCES.

By Margaret S. Libby. Columbia University Press, New York. $3.75. 8¾ x 6; 209; 1935.

It was inevitable that a man with the intellectual curiosity of Voltaire, living in an age of great scientific progress, should take a lively interest in the sciences. His *Elements of the Philosophy of Newton* contributed much to the spread in France of knowledge of the Newtonian system. Nor was Voltaire content with the rôle of popularizer of science. He busied himself with experiments in physics, on which he based an *Essay on Fire* which he hoped would win him admission to the Academy of Sciences. In biology he held to the old idea of the fixity of species and ridiculed such early evolutionists as de Maillet, while his best remembered contribution to geology is the flippant suggestion that the fossil shells found in the Alps had been dropped there by pilgrims. The book contains a bibliography of 22 pages and an index.

MAN THE UNIVERSE-BUILDER. *Backgrounds and Foundations of the Scientific Technique. First Revised Edition.*

By Richard E. Lee. The Williams & Wilkins Co., Baltimore. $3.00. 8½ x 5½; xix + 443; 1935.

In this textbook for an orientation course in the sciences their history and fundamental methodology are described as well as an account of the fundamental concepts on which present-day science is based. Particular attention is given to the development of the concept that energy in its two essential aspects of electricity and radiation is the fundamental stuff of the universe. The concept of evolution is also traced in both its cosmological and its biological applications. Suggestions for further reading and an index are given.

AN OPEN LETTER TO COLLEGE TEACHERS.

By Fernandus Payne and Evelyn W. Spieth. Principia Press, Bloomington, Ind. $3.25. 8¾ x 6; xiii + 380; 1935.

This book discusses and criticizes teaching in American colleges and universities today. The need for improvement is realized and changes are suggested. There is very little that is new, the material could have been more compactly organized, and the style is verbose. An extensive bibliography and a good index are included.

THE NEXT HUNDRED YEARS. *The Unfinished Business of Science.*

By C. C. Furnas. Williams & Wilkins Co., Baltimore. $3.00. 8½ x 5½; xiv + 434; 1936.

The Next Hundred Years, entertainingly written in the language of the layman, points out what the scientist has yet to accomplish and shows the deficiencies in science up to date. The book is divided into five parts: Biology, Chemistry, Physics, Engineering; and the whole discussion generally summed up in the final section, Social Consequences.

CAMBRIDGE READINGS IN THE LITERATURE OF SCIENCE. *Being Extracts from the Writings of Men of Science to Illustrate the Development of Scientific Thought.*

By William C. D. Dampier-Whetham and Margaret D. Whetham. The University Press, Cambridge; The Macmillan Co., New York. $1.00. 7¾ x 5½; xi + 275 + 8 plates; 1935.

The extracts in this book have been chosen to illustrate the development in the thought of succeeding ages of cosmogony from Genesis to Eddington, of the atomic theory from Lucretius to Rutherford, and of the theory of evolution from Aristotle to Bergson.

FRENCH SCIENCE *and Its Principal Discoveries Since the Seventeenth Century.*

By Maurice Caullery. French Institute in the United States, New York. $1.25. 7⅜ x 5; xi + 229; no date.

A review of this book in the original French will be found in THE QUARTERLY REVIEW, Vol. 9, page 258. This translation by the author is good except for the occasional retention of French word order and idioms.